SCIENTIFIC PUBLICATIONS OF THE AMERICAN MUSEUM OF NATURAL HISTORY
AMERICAN MUSEUM NOVITATES
BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
ANTHROPOLOGICAL PAPERS OF THE AMERICAN MUSEUM OF NATURAL HISTORY

PUBLICATIONS COMMITTEE
ROBERT S. VOSS, CHAIR

BOARD OF EDITORS
JIN MENG, PALEONTOLOGY
LORENZO PRENDINI, INVERTEBRATE ZOOLOGY
ROBERT S. VOSS, VERTEBRATE ZOOLOGY
PETER M. WHITELEY, ANTHROPOLOGY

MANAGING EDITOR
MARY KNIGHT

Submission procedures can be found at http://research.amnh.org/scipubs

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).

ON THE COVER: TRACHELOPACHYS CINGULIPES, MALE FROM PREDELTA NATIONAL PARK, ARGENTINA, HABITUS.

RAMÍREZ: DIONYCHAN SPIDERS

AMNH BULLETIN 390

2014

THE MORPHOLOGY AND PHYLOGENY OF DIONYCHAN SPIDERS (ARANEAE: ARANEOMORPHAE)

MARTÍN J. RAMÍREZ

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

THE MORPHOLOGY AND PHYLOGENY OF DIONYCHAN SPIDERS (ARANEAE: ARANEOMORPHAE)

MARTÍN J. RAMÍREZ
Division of Invertebrate Zoology,
American Museum of Natural History;
Museo Argentino de Ciencias Naturales,
Consejo Nacional de Investigaciones Científicas
y Técnicas,
Buenos Aires, Argentina

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 390, 374 pp., 231 figures, 37 tables
Issued June 27, 2014

Copyright © American Museum of Natural History 2014
ISSN 0003-0090

CONTENTS

Abstract 4
Introduction 5
  Aims and Scope 5
  Previous Phylogenetic Analyses and Background 6
  Selection of Representative Taxa 8
Material and Methods 9
  Specimens and Preparations 9
  Image Data Management 10
  Phylogenetic Data Management 10
  Phylogenetic Analysis Methodology 12
  Abbreviations 14
Morphology and Characters 15
  Carapace 15
  Eyes 23
  Chelicerae 36
  Mouthparts: Labrum, Labium, and Endites 54
  Female Palp 61
  Sternum and Pleural Area 71
  Legs 75
  Setae 122
  Abdomen: First to Third Segments 148
  Abdomen: Fourth to Sixth Segments 162
  Male Palp 210
  Female Genitalia 251
  Development and Behavior 273
Phylogenetic Analysis 276
Relationships of Outgroups 279
  The Divided Cribellum Clade 279
  The RTA Clade 279
Lycosoids and the Root of Dionycha 282
  The Oval Calamistrum Clade 283
  Tengellidae, Zorocratidae, Zoropsidae, and Ctenidae 285
  The Root of Dionycha and the Evolution of the Claw Tuft 292
Main Clades of Dionycha 294
  Corinnidae and Allies 295
  The Limits of Clubionids, Miturgids, and Eutichurids 296
  Miturgidae 299
  Eutichuridae 302
  Anyphaenidae and Other Groups with Complex Tracheae 306
  Clubionidae and Allies 309
  Sparassidae 310
  Selenopidae 312
  The Affiliation of Salticids and Crab Spiders 313
  Philodromidae 313
  Thomisidae 314
  Salticidae 320
  The Oblique Median Tapetum (OMT) Clade 322
  The *Teutamus* Group 327
  Lamponidae 328
  The Claw Tuft Clasper (CTC) Clade 328

  Trochanteriidae and Allies 330
  Gallieniellidae 331
  Trachelidae 331
  Phrurolithidae 335
  Cithaeronidae and Ammoxenidae 336
  Prodidomidae 336
  Gnaphosidae 338
Taxonomy 339
  Eutichuridae 340
  Miturgidae 341
  Trachelidae 342
  Phrurolithidae 342
  Liocranidae 343
  Corinnidae 344
  Clubionidae 344
  Tengellidae 344
Acknowledgments 344
References 346
Appendix 1. Material Examined 356

ABSTRACT

A phylogenetic analysis of the two-clawed spiders grouped in Dionycha is presented, with 166 representative species of 49 araneomorph families, scored for 393 characters documented through standardized imaging protocols. The study includes 44 outgroup representatives of the main clades of Araneomorphae, and a revision of the main morphological character systems. Novel terminology is proposed for stereotyped structures on the chelicerae, and the main types of setae and silk spigots are reviewed, summarizing their characteristics. Clear homologs of posterior book lungs are described for early instars of Filistatidae, and a novel type of respiratory structure, the epigastric median tracheae, is described for some terminals probably related with Anyphaenidae or Eutichuridae. A new type of crypsis mechanism is described for a clade of thomisids, which in addition to retaining soil particles, grow fungi on their cuticle. Generalized patterns of cheliceral setae and macrosetae are proposed as synapomorphies of the Divided Cribellum and RTA clades. Dionycha is here proposed as a member of the Oval Calamistrum clade among the lycosoid lineages, and *Liocranoides*, with three claws and claw tufts, is obtained as a plausible sister group of the dionychan lineage. The morphology of the claw tuft and scopula is examined in detail and scored for 14 characters highly informative for relationships. A kind of seta intermediate between tenent and plumose setae (the pseudotenent type) is found in several spider families, more often reconstructed as a derivation from true tenent setae rather than as a phylogenetic intermediate. Corinnidae is retrieved in a restricted sense, including only the subfamilies Corinninae and Castianeirinae, while the "corinnid" genera retaining the median apophysis in the copulatory bulb are not clearly affiliated to any of the established families. Miturgidae is redefined, including Zoridae as a junior synonym. The Eutichuridae is raised to family status, as well as the Trachelidae and Phrurolithidae. New synapomorphies are provided for Sparassidae, Philodromidae, and Trachelidae. Philodromidae is presented as a plausible sister group of Salticidae, and these sister to Thomisidae; an alternative resolution placing thomisids in Lycosoidea is also examined. The Oblique Median Tapetum (OMT) clade is proposed for a large group of families including gnaphosoids, trachelids, liocranids, and phrurolithids, all having the posterior median eye tapeta forming a 90° angle, used for navigation by means of the polarized light in the sky as an optical compass; prodidomines seem to have further enhanced the mechanism by incorporating the posterior lateral eyes to the system. The *Teutamus* group is recognized for members of the OMT clade that are usually included in Liocranidae, but not closely related to *Liocranum* or phrurolithids. The Claw Tuft Clasper (CTC) clade is proposed for a group of families within the OMT clade, all having a peculiar mechanism grasping the folded base of the claw tuft setae with a hook on the superior claws. The CTC clade includes Trachelidae, Phrurolithidae, and several gnaphosoids such as Ammoxenidae, Cithaeronidae, Gnaphosidae, and Prodidomidae. A remarkable syndrome involving the expansion of the anterior lateral spinnerets, often sexually dimorphic, is here reported for some Miturgidae and several members of the CTC clade, in addition to the known cases in Clubionidae and "Liocranidae." The following genera are transferred from Miturgidae to Eutichuridae: *Calamoneta*, *Calamopus*, *Cheiracanthium*, *Cheiramiona*, *Ericaella*, *Eutichurus*, *Macerio*, *Radulphius*, *Strotarchus*, *Summacanthium*, and *Tecution*; *Lessertina* is transferred from Corinnidae to Eutichuridae. The following genera are transferred to Miturgidae: *Argoctenus*, *Elassoctenus*, *Hestimodema*, *Hoedillus*, *Israzorides*, *Odomasta*, *Simonus*, *Thasyraea*, *Tuxoctenus*, *Voraptus*, *Xenoctenus*, *Zora*, and *Zoroides*, from Zoridae; *Odo* and *Paravulsor*, from Ctenidae; *Pseudoceto* from Corinnidae. The following genera are transferred from Corinnidae to Trachelidae: *Afroceto*, *Cetonana*, *Fuchiba*, *Fuchibotulus*, *Meriola*, *Metatrachelas*, *Paccius*, *Paratrachelas*, *Patelloceto*, *Planochelas*, *Poachelas*, *Spinotrachelas*, *Thysanina*, *Trachelas*, *Trachelopachys*, and *Utivarachna*. The following genera are transferred from Corinnidae to Phrurolithidae: *Abdosetae*, *Drassinella*, *Liophrurillus*, *Plynnon*, *Orthobula*, *Otacilia*, *Phonotimpus*, *Phrurolinillus*, *Phrurolithus*, *Phruronellus*, *Phrurotimpus*, *Piabuna*, and *Scotinella*. *Dorymetaecus* is transferred from Clubionidae to Phrurolithidae. *Oedignatha* and *Koppe* are transferred from Corinnidae to Liocranidae. *Ciniflella* is transferred from Amaurobiidae to Tengellidae.

INTRODUCTION

Many spider groups have lifestyles involving intense interaction with vertical and overhanging surfaces, such as the landscape posed by plant foliage, or the intricacies of the leaf litter, to mention a couple of prominent examples. These spiders are able to hunt or stalk their prey, without having to depend on a previously constructed silk structure. As it happens, they have evolved again and again the same biomechanic solution to that challenge: producing a pad of adherent setae at the tip of their legs, the claw tufts, and getting rid of the inferior tarsal claw (fig. 45B). A cursory examination of the distribution of such adherent setae (fig. 187) shows that there is little chance, if any, that they have a common evolutionary origin. As will be shown here, the tenent setae present many instances of convergences and reversions, yet the myriad details of their morphology and interaction with the claws are highly informative for the relationships of dionychan families.

Dionycha is a large and diverse group of 16–17 families of spiders, loosely defined by having only two claws on the leg tarsi, flanked by tufts of special setae that adhere to smooth surfaces. Dionychan spiders comprise about a third of the spider species known so far (Platnick, 2012). Little is known of their affinities, except that they belong in a large clade of araneomorph spiders with separate fertilization ducts and a projection on the male palpal tibia (the RTA clade of Entelegynae; see Coddington et al., 2004). The monophyly of Dionycha was not tested in quantitative analyses, except by the inclusion of a few representatives, mainly as outgroups (e.g., Silva Davila, 2003; Miller et al., 2010). The name was introduced by Petrunkevitch (1928) for ecribellate araneomorphs with two tarsal claws and one tracheal spiracle, and later he (1933) restricted the group to those having claw tufts and three pairs of cardiac ostia as well (table 1). Subsequent authors have roughly followed Petrunkevitch's classification, until the work of Lehtinen (1967) changed the understanding of araneomorph diversity of those times. Lehtinen touched tangentially on dionychan families, but introduced significant modifications. Faithful to his declared aim of open-mindedly rethinking higher relationships and reassessing the composition of families, he distributed the large "Clubionidae" of those times in several superfamilies, and raised to family level the Liocranidae, Miturgidae, and Corinnidae. Most of those changes were followed by or greatly influenced today's classifications. Other proposals, such as the relationships of Phrurolithinae with gnaphosids were not generally accepted then, but are supported in the analysis here presented. Lehtinen did not even consider such a group as Dionycha, but rather considered multiple parallel losses of the third tarsal claw (1967: fig. 3). He distributed the dionychan families among several superfamilies in the two main branches Amaurobiides (Amaurobioidea, Gnaphosoidea, Sparassoidea, Lycosoidea) and Zodariides (Zodarioidea, Salticoidea, Thomisoidea). It is hard to further discuss Lehtinen's ideas using current phylogenetic argumentation. For example, his Amaurobioidea is admittedly paraphyletic, containing all the basal members of the remaining superfamilies of Amaurobiides, and his tables of characters are too vague for diagnostic identification (Lehtinen, 1967: fig. 11, table 7). Although the phylogenetic analyses of the last 20 years (table 2) are, in comparison, more precise and accessible for discussion, the ever-changing results of phylogenetic hypotheses of the RTA clade, Lycosoidea, and—why not?—Dionycha, all show that we are just beginning to work our way in making order of the higher level groups of Entelegynae.

AIMS AND SCOPE

The design of this study has the following objectives in mind: (1) test the monophyly of Dionycha, or discover the main dionychan lineages; (2) find the closest relatives and internal rooting of dionychan lineages; (3) clarify the relationships among families of dionychans; (4) test the monophyly and composition of some large and little studied dionychan families, especially Liocranidae, Corinnidae, and Miturgidae; (5) build a coherent system of morphological homologies tested for all dionychans and representatives of the main clades of Araneomorphae;

TABLE 1

Historical concepts of Dionycha

Approximate distribution of current families in historical concepts of Dionycha and equivalent groups. Symbols: + = Dionycha; × = not considered; − = not existing at that time.

Family	Petrunkevitch, 1928	Petrunkevitch, 1933	Bristowe, 1938: section C	Roewer, 1955	Coddington et al., 2004	Jocqué and Dippenaar-Schoeman, 2006	Silva Davila, 2003
Ctenidae	+	+	+	+			
Zoropsidae	+	+					
Zoridae	+	+	+		+		
Miturgidae (Miturginae)	−	−	−	−			
Miturgidae (Eutichurinae)	−	−	−	−	×	×	+
Homalonychidae	+	+	+	+	×	×	×
Gallieniellidae	−	−	−	−	+	+	×
Cithaeronidae	−	−	−		+	+	×
Trochanteriidae	+	+	+	+	+	+	×
Ammoxenidae	+			+	+	+	×
Lamponidae	−	−	−	−	+	+	×
Prodidomidae	+		+	+	+	+	×
Gnaphosidae	+	+	+	+	+	+	×
Liocranidae	+	+	+	+	+	+	+
Philodromidae	+	+	+	+	+	+	×
Corinnidae	+	+	+	+	+	+	×
Anyphaenidae	+		+	+	+	+	×
Clubionidae	+	+	+	+	+	+	+
Sparassidae	+	+	+	+	+	+	×
Selenopidae	+	+	+	+	+	+	×
Thomisidae	+	+	+	+	+	+	×
Salticidae	+	+	+	+	+	+	×

and (6) trace the evolution of character systems important in the evolution of Dionycha.

Previous Phylogenetic Analyses and Background

So far, all the phylogenetic analyses of Araneomorphae produced unstable, weakly supported group hypotheses for the higher-level relationships, and this study is no exception. We may as well begin to consider that this is a real pattern, rather than a limitation of current methods and data sources. That is, even if we find a robust phylogeny (e.g., using thousands of molecular markers and morphological characters), the homoplasy levels of the biologically interesting features might be so high that the tracing of their origin would be uncertain anyway. The following is a brief account of the previous phylogenetic analysis used to guide the selection of representatives (see fig. 187).

Main Clades of Araneomorphae: The landmark study of Platnick et al. (1991) was extremely encouraging at the time, because it obtained quantitative phylogenetic evidence for higher groups such as Araneoclada, Austrochiloidea, Haplogynae, and Entelegynae. Subsequent analyses and new findings of morphological, behavioral, and molecular data revealed that the situation is much more complex than previously thought. The following four cases are crucial for this instability: (1) Austrochilines turned out to have presumably derived characters such as cylindrical gland spigots, both legs moving while combing cribellate silk, and median tracheae (Griswold et al., 2005; Lopardo et al., 2004; Ramírez, 2000); (2) a suite of primitive

TABLE 2
Legacy datasets
Previous cladistic analyses with characters relevant for the placement and internal resolution of Dionycha and the outgroups used here.

Analysis	Coverage
Baehr and Baehr, 1993	Hersiliidae
Bosselaers and Jocqué, 2000	Hortipes
Bosselaers and Jocqué, 2002	Liocranidae
Coddington, 1990	Orbiculariae
Davies, 1998	Metaltellinae
Davies, 1999	RTA clade
Griswold, 1993	Lycosoidea
Griswold et al., 1998	Araneoidea
Griswold et al., 1999, 2005	Entelegynae
Hormiga et al., 1995	Araneoidea
Jocqué, 1991	Zodariidae
Platnick et al., 1991	Araneomorphae
Platnick, 2000, 2002	Gnaphosoidea
Ramírez, 2000	Araneomorphae
Ramírez and Grismado, 1997	Filistatidae
Ramírez 1995, 2003	Anyphaenidae
Raven and Stumkat, 2005	Lycosoidea
Rodrigo and Jackson, 1992	Spartaeinae
Schütt, 2002	Orbiculariae, Palpimanoidea
Schütt, 2003	Araneoidea
Silva Davila, 2003	Lycosoidea
Wijesinghe, 1997	Salticidae

conditions were found in Filistatidae, such as M-shaped intestine, only leg IV moving while combing, and the presence of posterior book lung leaves in early juveniles (Griswold et al., 2005; Eberhard, 1988; Lopardo and Ramírez, 2007; this study); (3) several members of Palpimanoidea (Forster and Platnick, 1984) turned out to be nested inside Araneoidea (Schütt, 2000, 2002; Griswold et al., 2005; Rix et al., 2008; Blackledge et al., 2009; Lopardo et al., 2011); and, lastly and more surprisingly, (4) the leptonetid *Archoleptoneta schusteri*, supposedly well nested in the ecribellate Haplogynae, revealed a full-fledged cribellum and calamistrum (Ledford and Griswold, 2010).

ENTELEGYNAE AND THE RTA CLADE: Besides the extensive analyses made on of orb-weavers (see table 2) and the ticking time bomb of Palpimanoidea, the analyses of Griswold et al. (1999) and Griswold et al. (2005) began the cladistic exploration of the main branches of entelegynes other than orbicularians or palpimanoids. Major new hypotheses of those works are the eresoids (Oecobiidae + Eresidae), titanoecoids (Titanoecidae + Phyxelididae), and the Fused Paracribellar clade (a group of families related to Amphinectidae and Desidae). Those were followed shortly thereafter by the molecular analyses of Spagna and Gillespie (2008) and Miller et al. (2010). This last analysis did not recover eresoids, and placed the titanoecoid representatives well within the RTA clade, but obtained an Austral Cribellate clade (Spagna and Gillespie, 2008) fairly similar to the Fused Paracribellar clade but including the Stiphidiidae. Both molecular studies suggest that the RTA clade should include at least the Dictynidae.

LYCOSOIDEA AND RELATIVES: Griswold (1993) made the first quantitative analysis exploring the relationships of the groups of families allied to wolf spiders, as proposed by Lehtinen (1967) and Homann (1971). The candidates for such a group usually have some striking characters: grate-shaped tapeta, oval calamistrum, tibial cracks on male legs, and a tegulum-subtegulum interlocking mechanism in the male copulatory bulb. The group endured some further analyses based on morphology (Griswold et al., 2005; Silva Davila, 2003), although the internal relationships of lycosoids and relatives (the Oval Calamistrum clade in Griswold et al., 1999, 2005; the Grate-Shaped Tapetum clade in Silva Davila, 2003) are fluctuating in the different analyses (Griswold, 1993; Silva Davila, 2003; Raven and Stumkat, 2005).

THE ROOT OF DIONYCHA: Recent molecular analyses of the RTA clade (Miller et al., 2010; Spagna and Gillespie, 2008) suggested that the dionychans may be the sister group to the lycosoids, although those studies had only a limited number of representatives of those clades (three and one, respectively). Similarly, Silva Davila (2003) found Dionycha as sister to a Grate-Shaped Tapetum clade; in her analysis, the five representatives of Dionycha were joined by only one character, the precoxal sclerites (see fig. 199A).

DIONYCHAN RELATIONSHIPS: The first comprehensive study of dionychan relationships is an unpublished dissertation by Penniman (1985), including five families (Clubionidae, Anyphaenidae, Gnaphosidae, Corinnidae and Liocranidae). His analysis was based on a small number of characters, scored for groundplans of families or subfamilies, instead of representative species. Several of Penniman's characters were challenged in the last decade, and his analysis would nowadays be insufficient, but there are some coincidences with more recent studies. The clade corresponding to Dionycha in Silva Davila's (2003) tree is supported by the precoxal sclerites discovered by Penniman. Phrurolithinae was placed in Corinnidae, and Gnaphosidae appeared as the sister group of a clade consisting of Corinninae, Castianeirinae, Trachelinae, and Phrurolithinae, which has some coincidences with the results obtained here. Further cladistic analysis of dionychan spiders have focused in the relationships of Gnaphosoidea, corinnids, and liocranids. The successive studies of Gnaphosoidea (Platnick, 2000, 2002) centered on the amazing Australian diversity, consolidated the relationships and delimitation of families outlined by Platnick (1990), mostly from the morphology of spinnerets and spigots. The analysis by Bosselaers and Jocqué (2002) produced novel or unexpected groupings, of which one was considered sufficiently well supported to make the transfer of Phrurolithinae to the family Corinnidae, close to Trachelinae; the liocranids were somehow dispersed through the tree, and Castianeirinae did not appear related to corinnids. Several representatives from such analysis were further combined with gnaphosoids and additional trachelines in a recent cladistic analysis (Haddad et al., 2009), also led by Jan Bosselaers. As a result, the phrurolitines still held somehow in the vicinity of trachelines, this time near Castianeirinae as well, and the liocranids continued to be polyphyletic, and were also mixed with gnaphosoids.

SELECTION OF REPRESENTATIVE TAXA

While selecting representatives for the phylogenetic analyses, an effort was made to include (1) type genera of families and subfamilies while (2) maximizing overlap with previous phylogenetic studies and (3) using well-known representatives, (4) especially those near the base of the clade they represent. Further representatives of dionychans were also selected according to (5) the availability of well-preserved specimens. The taxon sampling is summarized over a schematic representation of gross phylogenetic hypotheses of araneomorph spiders at the time of starting this project (fig. 187).

"OUTGROUPS": From the beginning of this study it was clear that Dionycha might not be a monophyletic group, hence the selection of outgroup taxa had to be sufficiently ample to allow for a real test of monophyly (44 out of 166 taxa, or 27%, are outgroups). The dataset includes representatives of the main lineages of the RTA clade, as well as of the main basal clades of Araneomorphae, the outgroups of the RTA clade itself. Previous analyses (Griswold et al., 1999, 2005) explicitly favored the inclusion of cribellate, presumably plesiomorphic representatives of the main RTA clades. Since dionychans are ecribellate, finding the closest relatives and internal rooting of dionychan lineages, the selection of representatives had to include ecribellate members as well. Lycosoids are especially well represented, since several dionychan groups have a grate-shaped tapetum (thomisids), and some were explicitly included among lycosoids (zorids, some miturgids). This ample taxonomic coverage allowed for a detailed review of the morphological homologies and the legacy characters relevant to dionychans. Some representatives of "zodarioids" (*Homalonychus*, and the zodariids *Cyrioctea*, *Cybaeodamus*, *Storenomorpha*, and *Cryptothele*) were studied in detail but not included in the final dataset, because although monophyletic, they were extremely unstable in the analyses.

"INGROUP": All families putatively members of Dionycha were considered in this analysis, including those that were placed within Lycosoidea. To study the relationships among families of dionychans, more than one or two members were studied for each family whenever possible, trying to sample their internal diversity. This study devoted more effort in three large dionychan families with contentious limits (Liocranidae, Corinnidae, and Miturgidae, 52 representatives in total), at the expense of a less-dense coverage of the gnaphosoid families (28 representatives), which had received focused and detailed attention in recent years (Platnick, 2000, 2002). Whenever possible, the sampling of representatives was inspired by previous phylogenetic analyses and classification in subfamilies.

GEOGRAPHY: The taxa studied here are a fairly good representation of the global taxonomic breath of the families involved. A few regions were slightly favored because of the availability of good recent collections (such as those of Vietnam, thanks to the work of Diana Silva Dávila, and Argentina), but the sampling is not systematically biased toward a given biogeographical region, continent or hemisphere.

MATERIAL AND METHODS

SPECIMENS AND PREPARATIONS

The specimens used for this study were dissected and prepared in a mostly stereotyped sequence, depending on their number and state of conservation. The techniques employed are summarized below. All preparations resulting in images, either permanent or temporary, were assigned a unique alphanumeric preparation identifier (MJR-####), and their data stored in an MS-Access database, which served to record image metadata (see below).

SEM PREPARATIONS: By default, each species resulted in about eight scanning electron microscopy (SEM) preparations (female: left chelicerae, left palp, left legs I and IV, epigyne digested, spinnerets; male: left palp, abdomen). The most critical step for obtaining neat SEM preparations was selecting clean, well-preserved specimens from collections. While still in alcohol, all samples were brushed using a thin painting brush of synthetic fibers, following the direction of the setae. Very dirty samples, especially of hard structures such as the male copulatory bulb were cleaned for a few seconds in an ultrasonic cleaner. Before drying, some hairs had to be removed with fine forceps to expose structures (figs. 45B, 120B, 128F). All samples were critical-point dried after dehydration in ethanol series. Each sample was mounted on a separate aluminum stub, using adhesive carbon tabs (fig. 15A, background) or adhesive copper tape (fig. 11E, bottom right). During the mounting, some further depilation was made with fine forceps, the loose hairs or dirt then removed with brush and a jet of air blowing through a thin pipette connected to a rubber tube. To allow for a better conductivity, once positioned on the adhesive medium, the borders of the pieces were glued to the conductive substrate with colloidal graphite on isopropanol base (fig. 11E). Such conductive paint reduces the charging of the sample under the SEM, and further secures the piece. The preparation identifier was engraved on each stub with a needle, to make it visible in the SEM monitor.

KOH DIGESTION: The respiratory system and spermathecae of haplogynes were examined after digestion in a hot 10%–20% KOH solution. The pieces were placed in a double boiler and heated in a hot plate or a Fuyí© heater for antimosquito tablets. After digestion, cleaning, and passing through ethanol, the samples were usually stained by quickly immersing in a saturated solution of chlorazol black in ethanol. The dissections were made as described in Platnick et al. (1999). Smaller samples (spiderlings, minute spiders) were digested inside a glass microvial with a loose cotton stopper, to prevent losing the specimens when they become transparent. In that case, the changes of fluids and staining were made through the cotton, under a stereomicroscope. Manipulation of digested pieces under the stereomicroscope was made with reflected dark field illumination, especially for the delicate pieces; this was done by placing a mirror below the Petri dish used for the samples. The digested pieces were observed in lactic acid with compound microscope on an excavated slide, using a strip cut from a glass cover to retain the sample in position.

ENZYME DIGESTION: Spermathecae were cleaned of soft tissues for SEM preparation using enzymatic digestion. The dissected epigyne was placed on a small vial with water and trypsin, and incubated at 40° C overnight. Some samples were digested in pancreatine and borax solution, as in Álvarez et al. (2008).

CLOVE OIL CLARIFICATION: Temporary clarification of soft structures was made with clove oil. As usual, this was applied to examine spermathecae without digesting, but also to expose the path of the spermophor in the male copulatory bulb. Eye tapeta were observed after overnight clarification of the whole specimen or carapace in clove oil; the specimens used for dissection of chelicerae were convenient for clarification, since the oil can quickly penetrate into the cephalic area once a chelicerae is removed.

KOH EXPANSION OF MALE COPULATORY BULB: The palps were dissected and brushed, sometimes sonicated, but not depilated. The expansion was made in a manner similar to Shear's (1967). The palp was placed in a 10% KOH solution for some minutes, up to half an hour, and then cycled between KOH solution and distilled water until fully expanded. Larger or harder palps needed longer cycles; in those cases the heat of a lamp in the distilled water phase was used to help expansion.

IMAGE DATA MANAGEMENT

IMAGE MEDATATA: Image files were named starting with the preparation code (e.g., abbreviated "686aILeft claws female Lyssomanes.tif," or verbose, "MJR1213e Claws I apical ff Paradiestus.tif"). Using this convention, all the specimen metadata could be easily retrieved from the preparations database. Images and their data were maintained in an IMatch database (www.photools.com). SEM settings and other device-generated metadata were imported parsing the buddy text files (Hitachi SEM, Leica stereomicroscope) or embedded EXIF metadata (FEI SEM) using custom scripts. All images were recorded with a scale bar. For light microscopy devices that lacked scale-bar functions, the magnification was encoded in the file name between brackets (e.g., "MJR1237_01[Nx3] carapace dors ff Doliomalus.jpg"), and a calibrated scale was then overlaid on the image using a custom script in IMatch. The image metadata elements correspond to those used in Morphbank (http://morphbank.net) plus some additional fields developed for the ATOL Spiders project (Ramírez et al., 2007), including identifiers for a web-based resource tool, the Spider Ontology (Ramírez, 2011). To allow for a quick orientation, images of spinnerets are labeled in figures with the position marked on a schematic map of the spinnerets (e.g., fig. 119, top left of each image).

IMAGE REPOSITORY: Since the scoring of the dataset depends heavily on high-resolution images (about 30% of the characters in this dataset can be scored only from SEM images), and it is impossible to publish all of them in this paper, the image repository is an important part of the documentation of this study. All the images produced for this study and their corresponding metadata are deposited in Morphbank collection ID 799551 (http://www.morphbank.net/myCollection/?id=799551), openly accessible in full resolution under Attribution-Noncommercial-Share Alike 3.0 Creative Commons license.

PHYLOGENETIC DATA MANAGEMENT

In this study the raw phylogenetic dataset was used as a research tool to collect observations, comments, questions, and workflow tags, and to test experimental characters, homology hypotheses, and covariations, in a stereotyped yet open-minded way. As the study progressed, the analyzable datasets were downstream products, derived each time as a subset of the raw dataset. For analysis, pseudocharacters (see below) and rejected characters were deactivated, as well as certain dataset rows or columns used for workflow tags and storage of comments. These operations were automated through custom scripts written for TNT (Goloboff et al., 2008a). The dataset used for analysis is listed in table S1 (see supplementary data: http://dx.doi.org/10.5531/sd.sp.4). A data package containing the phylogenetic dataset and character statistics can be found in the Dryad repository (Ramírez, submitted.); the phylogenetic dataset is also deposited in TreeBase with accession number 14043. The phylogenetic dataset was edited and maintained in Winclada (Nixon, 1999), with several iterations of manual edition in plain text format.

CELLS: Scoring of dataset cells was done from actual examination of specimens or their images. Only in exceptional cases the scoring was taken from the literature, and in that case a comment was inserted indicating the source. A few characters from soft internal anatomy were scored entirely from the literature; in those cases, only primary sources were used. Polymorphisms (i.e., more than one character state assigned to a cell) were used to express variability, intermediacy, or ambiguity in the anatomical observation, and the case was explained in a comment.

LEGACY CHARACTERS: The first step for the building of the phylogenetic matrix was reviewing the characters previously used in the literature. Table 2 summarizes the previous cladistic analyses considered as sources of legacy characters relevant for the placement and internal resolution of Dionycha in Araneomorphae. Legacy characters were sorted by body region in a preliminary schema, which ended up as the skeleton of the Spider Ontology. Characters expressing equivalent evolutionary transformations were grouped together and more generally reformulated. For example, legacy characters expressing the curvature of eye rows ("straight/procurved," "straight/recurved") were condensed as a multistate character ("procurved/straight/recurved"). The sorting and condensing of legacy characters involved a critical review of the underlying homology hypotheses. Characters used for species-level phylogenies that are known to be very variable were not considered for this higher-level analysis. In this category fell most of the species-specific genitalic characters, such as number of coils of the male palpal embolus or the female copulatory ducts.

CHARACTER HYPOTHESES AND PSEUDOCHARACTERS: Characters were reviewed and reformulated many times during this study, to accommodate newly found variation or revised anatomical interpretations. Special effort was placed in using the cell comments as supporting documentation for the decisions involving the reformulation or rejection of characters, and preserving finely grained observations independent of the grouping into coarsely defined character states. The following informal rules were used for the maintenance and documentation of characters, according to the capabilities of Winclada:

1. If a character was found to contain an erroneous anatomical interpretation (e.g., states 0 and 1 refer to nonhomologous structures), a brief note was inserted explaining the case, and the column was moved to the end of the dataset. Previous scorings and comments remained, but the character was not visited again.
2. If a character accumulated many polymorphic scorings due to intermediate conditions, it was usually sent to the end of the dataset and no longer considered.
3. If an observation did not fit well in any of the character states, the cell was scored as polymorphic or left inapplicable, and a comment explaining the situation was inserted in the cell.
4. After accumulation of several problematic scorings, the character was reviewed and redefined using the cell comments as guidelines.
5. Complex or very variable structures were often loosely scored in "pseudocharacters," columns of the dataset used to accumulate potential character states and cell comments (e.g., patterns of distribution of PMS cylindrical gland spigots, 30 "states" in three columns). These pseudocharacters were then used as guide for the creation of regular phylogenetic characters; in many cases the derived characters could be scored without having to reexamine the specimens. After recoding in new characters, many of those pseudocharacters continued to be scored upon the addition of new taxa.
6. Finely grained characters that were recoded in a simpler character (e.g., by grouping together two or more states into one state, such as joining male and female characters into one) were left in the dataset and continued to be scored. In this way, the finely grained observations are still available for further experiments (e.g., testing the correlation of male and female scorings).
7. Structures of interest were placed in the dataset with only one state, to force its examination. New states were subsequently added if necessary. This strategy was very productive for the learning and documentation of the anatomy and resulted in several new characters.

INVARIANT CHARACTERS: Many invariant characters, which are phylogenetically uninformative within the current dataset, were kept in the matrix for documentation purposes. As shown in Ramírez et al. (2007), one of the impediments for adequate merging of phylogenetic data from multiple sources is the lack of documentation of characters considered "not informative" for a given analysis and thus not scored in the study.

ANATOMICAL TERMINOLOGY: An effort was placed to map anatomical concepts and characters to terms in the Spider Ontology. Several new structures were discovered during this study, and those were added to the reference ontology. To avoid confusion with the usage of morphological terms and anatomical interpretations, the main character systems are preceded by a short description of the general morphology using a few fully labeled exemplar images.

TERMINAL TAXA AND SPECIMENS: This analysis uses species as terminal taxa, although they are referred to by genus in the text; binomial names are used when more than one species is included, or for species whose generic placement is questioned or uncertain (e.g., *Stephanopis ditissima*, *Odo bruchi*). Occasionally some scorings and interpretations are complemented from observations from additional species, and this is noted in the comments section for each character. Two of the terminals (*Ammoxenus* and *Zorocrates*) were scored from two different species (one species for male, another for female), in the first case for availability of specimens, in the second because the taxonomy of the genus was solved when this project was already advanced. Species and voucher specimens examined for this study are detailed in appendix 1. Labels have been added to the vials (e.g., "Voucher for Dionycha study, M. Ramírez, 2000–2008"). The end dates in those labels varied as the timeline was postponed according to newly added terminals.

PHYLOGENETIC ANALYSIS METHODOLOGY

Phylogenetic analyses were made using TNT (Goloboff et al., 2008a). Most of the operations were programmed in scripts, so they can be documented and replicated upon changes in the dataset.

IMPLIED WEIGHTING AND SENSITIVITY: The dataset was analyzed under 10 different weighting regimes: equal weights, and implied weights (Goloboff, 1993) with increasing constant of concavity $k = 3, 6, 9, \ldots, 27$. The results are shown on a preferred tree corresponding to an intermediate concavity with $k = 9$, which had the most groups in common with all the remaining weighting schemes (table 7). For each group, the number of weighting regimes where it is monophyletic was graphically represented as explained in figure 186. The election of weighting of characters against homoplasy rests on the experiments made in Ramírez (2003) and especially Goloboff et al. (2008b), finding a better performance when compared with analyses under equal weights; at any rate, sensitivity to changes in weighting regimes results in a lack of robustness.

TREE SEARCHES: For this dataset, traditional searches (e.g., 1000 replications of RAS+TBR) never hit the optimal scores, and the parsimony ratchet (Nixon, 1999; 100 replications of RAS+TBR+RAT, with 100 ratchet iterations) rarely did so. For each concavity, the dataset was analyzed using the new technologies of TNT, using sectorial searches, tree-drifting, and tree-fusion with the following commands and parameters (thanks to Pablo Goloboff for suggestions):

```
sec : xss 3+3-1 gocomb 10 combstart 5 fuse
  3 drift 6 ;
drift : rfit 0.10 num 150 nogiveup ;
xmult = hits 4 rep 5 drift 20 fuse 6 gfuse 4 ;
```

Subsequent searches with the preferred concavity resulted in 100 hits, at a rate of one hit every 30 seconds using a 2.8 GHz personal computer. With this rate of convergence on the same result, it is likely that the optimal tree was found.

BREMER SUPPORT: Bremer support (BS; Bremer, 1994) values were heuristically estimated performing TBR swapping from the optimal trees, retaining suboptimal trees with increasing bounds, up to 51,000 trees. BS values are expressed in terms of fit, under concavity constant $k = 9$, and are graphically displayed on branches according to the key in figure 186. To obtain greater precision, the weight of all characters was set to 100 (command "*ccode/100 . ;*"). Initial searches estimated a maximum value of BS = 90. A script then ran several cycles, increasing the tree buffer to 3000 trees each cycle, increasing the suboptimal bound each time. Given the complexity of the dataset, some Bremer values may be overestimated. An additional analysis without collapsing branches (command "*collapse = 0;*") for low suboptimal values was used to correct some overestimations in the weakly supported groups.

RESAMPLING SUPPORT MEASURES: An estimation of the support upon resampling was made using 1000 pseudoreplicates of jackknifing under symmetrical resampling (Goloboff et al., 2003), each with an intermediately aggressive search (two replicates of RAS+TBR+RAT+Fusing). Absolute frequencies greater than 55% are graphically displayed along with sensitivity and Bremer support values (fig. 186).

GRAPHICAL REPRESENTATION OF SENSITIVITY AND SUPPORT MEASURES: The two measures of support (Bremer and jackknifing) and the stability of groups to changes in weighting regimes was summarized as a compound measure represented as branch lengths (fig. 186) (see Giribet, 2003). To recover support values for the weakly supported groups, the Bremer support was represented in a logarithmic scale.

SYNAPOMORPHIES: Synapomorphy lists were produced by taking into account only the unambiguous changes in ancestral states (e.g., 0 → 1, but not 01 → 1; 01 → 2, but not 01 → 12). Because synapomorphy lists for polytomies in consensus trees are dependent on all the optimal resolutions, all optimal dichotomous trees were first calculated, producing lists of synapomorphies that are common to all of them (Common Synapomorphies command in TNT, "*apo[- ;*"). A conservative estimation of the synapomorphies was made using the same procedure but considering all resolutions suboptimal by 0.01 units of fit (that is, collapsing any group of BS = 0.01 or lower). The synapomorphies and groups that are lost after such operation are presented in parentheses (see table 11).

EVALUATION OF ALTERNATIVE RESOLUTIONS: Traditional groups or otherwise interesting hypotheses not found in the preferred trees were evaluated through constrained analyses, listing which characters would support or contradict such a resolution. First, a tree search was made with constraints forcing the monophyly of the group under evaluation, and the total fit difference was calculated with respect to the optimal tree. To estimate the character support against and in favor of alternative resolutions, the total fit difference is decomposed into the individual change of fit for every character. Characters that decrease their fit under the alternative resolution are in favor of such a grouping, and those that increase their fit oppose the group. The proportion of opposing and supporting characters is then calculated as C/F, where F is the sum of fit of all characters favoring a group, and C of those opposing it (Goloboff and Farris, 2001). Because constrained trees are always suboptimal, C/F is greater than 1. Values of C/F near 1 indicate that the constrained resolution is allowing almost as many characters to perform better, thus recovering a secondary signal in the data (fig. 206A). Conversely, large values of C/F indicate that such secondary signal is much smaller than the dominant one (fig. 206B, C). Because the lists of supporting and opposing characters may be extensive, only the characters adding most to the 75% of the range of F and C are reported.

ORDERED MULTISTATE CHARACTERS: Multistate characters were considered as ordered (= additive), according to the following general rules (see table S2, see supplementary data: http://dx.doi.org/10.5531/sd.sp.4):

(a) Nested states: A state definition implies the existence of a more general state: examples are "pronounced mound absent" – "present" – "mound plus dark long tooth"; "retrocoxal hymen absent" – "on leg I" – "on legs I–II" – "on legs I–III." This case is unproblematic, as the multistate character could have been scored as two or more binary characters with well defined homologies.

(b) Continuous: The character states have an obvious continuous basis; examples are "anterior eye row procurved" – "straight" – "recurved"; "female tarsi curvature straight" – "slightly bent" – "strongly bent to coiled." This cost regime follows all the methodological literature on continuous characters (e.g., Wiens, 2001; Goloboff et al., 2006).

(c) Intermediate: A character state is a plausible intermediate consistent with phylogenetic hypotheses or ontogenetic evidence: "two major ampullate gland spigots" – "one plus nubbin" – "one, no nubbin." This cost regime relies on previous knowledge that may not apply to the whole tree (in the example, from Townley and Tillinghast, 2003, 2009). Not all morphological intermediates were considered as ordered. For example, the claw tuft setae (char. 163) could be construed as an

ordered series "plumose" – "pseudotenent" – "tenent"; however, the results obtained here indicate that such a transformation series is not likely (fig. 198B).

(d) Gradual loss or gain: One of the states is "absent," and another is a plausible intermediate for the loss or gain, as in the case of relictual structures: "palpal claw present" – "reduced to nubbin" – "absent"; "inferior tarsal claw large" – "small" – "absent"; "precoxal triangles, absent" – "fused to sternum" – "separate from sternum." As in the examples above, these transformation costs rely on previous hypotheses that may be heterogeneous in the analysis. For example, the gradual palpal claw reduction is well documented in Salticidae, but not so in haplogynes. A binary scoring of this type of characters will usually score some cells as inapplicables, loosing the hypothesis of intermediacy.

(e) Counts: The character describes variation in number of discrete elements, without clear homology between each of the elements: "no tarsal trichobothria" – "single row" – "two or three rows"; "many Cy spigots" – "six" – "five" – "four" and so on. This is perhaps the most problematic case, as transformations of potentially nonhomologous structures may be conflated under the same state (e.g., the gain of basal and distal teeth, of mesal and ectal Cy spigots). Moreover, when counts are represented with several states, they may have a heavy impact on the analysis.

The five cases above are sorted from less to more contentious. In order to evaluate the impact of different treatments on the results, a few additional analyses were run with changes in the cost regimes, as in table 3.

Abbreviations

Ac	aciniform gland spigot
Ag	aggregate gland spigot
AT	anal tubercle
BG	Bennett's gland
C	conductor
Cb	cymbium
CbGv	cymbial groove
CbRMP	cymbial retromedian process
CD	copulatory duct
CG	cuticular gland
Ch	chemosensory seta
CO	copulatory opening
Cr	cribellum
CTC	claw tuft clasper
CwL	claw lever
CwS	claw slit sensilla
CwSt	claw-slit suture
Cy	cylindrical gland spigot
E	embolus
EBP	basal process on embolus
EF	epigastric furrow
FD	fertilization duct
FgS	fang shaft serrula
Fl	flagelliform gland spigot
Fu	fundus
Hr	tactile hair
ITC	inferior tarsal claw
LL	epigynal lateral lobe
MA	median apophysis
MaAm	major ampullate gland spigot
Mc	macroseta
MF	median field
MiAm	minor ampullate gland spigot
ML	epigynal median sector or lobe
MPg	mating plug
MS	modified PLS spigot (including pseudoflagelliform gland spigot)
MtS	metatarsal stopper
Nu	nubbin (except as noted, of ampullate gland spigot)
Pc	paracribellar spigot
Pcb	paracymbium
PEB	process on embolar base
PEs	promarginal escort seta
Pi	piriform gland spigot
PsTe	pseudotenent seta
REs	retromarginal escort seta
Rk	promarginal rake seta
RTA	retrolateral tibial apophysis
S1	primary spermatheca
S2	secondary spermatheca
Sc	scale (seta)
St	subtegulum
STC	superior tarsal claw
T	tegulum
Te	tenent seta
TO	tarsal organ
Tp	tartipore (except noted, of ampullate gland spigot)
TrSp	tracheal spiracle
UE	uterus externus
VSO	vibration sense organ on metatarsus
VTA	tibial ventral apical apophysis
Wh	cheliceral whisker seta

TABLE 3

Ordering of multistate characters

Experiments were made of sets of characters with ordered states (a–e), and three alternative cost schemes. U = unordered states. In experiment 9, * signifies that the characters are considered unordered when $Lu/Lo < 0.66$, where Lu is the length of characters with unordered states, and Lo is the length with ordered states, both calculated on the preferred tree (fig. 188). This index evaluates the departure from an ordered transformation series (i.e., a Lu/Lo value of 1 means there is a perfect fit to an ordered transformation series). See Phylogenetic Analysis Methodology for discussion.

	Experiment									
	0	1	2	3	4	5	6	7	8	9
(a) Nested		U								*
(b) Continuous			U						U	*
(c) Intermediate				U				U	U	*
(d) Gradual					U		U	U	U	*
(e) Counts						U	U	U	U	*

MORPHOLOGY AND CHARACTERS

CARAPACE

The carapace is the dorsal sclerotized shield of the cephalothorax (fig. 1A). The anterior part bearing the eyes is the cephalic area or caput. The thoracic area is often delimited anteriorly by the most anterior thoracic furrow corresponding with the underlying leg muscles. The lateral and posterior margins of the carapace are often bordered by a reflexed sclerotized strip, usually more reflexed on the posterior margin. The clypeus is the stretch of carapace between the eyes and the anterior margin of carapace. There may be a sclerite articulate with the clypeal margin, the chilum, which may be divided into two halves (fig. 3A).

0. Thoracic fovea or apodeme: 0. Absent. The insertion of the thoracic muscles occurs on a smooth or slightly depressed internal cuticle area (fig. 1B–D). 1. Present (figs. 1A, 2A–C). Sometimes a thin apodeme can be inferred externally as a longitudinal dark line, even when the cuticle is externally smooth (fig. 3B). COMMENTS: *Oecobius*, *Stegodyphus*, *Cebrenninus*, *Geraesta*: just a depressed area (scored 0).

1. Thoracic fovea shape: 0. Wide depression (fig. 2D). This occurs in some basal members of Araneomorphae and Entelegynae (*Hypochilus*, *Eresus*, *Araneus*, Nicodamidae and *Titanoeca*), and *Cheiracanthium*, one of the few Eutichuridae (together with *Strotarchus*) with thoracic fovea. 1. Deep pit (fig. 2G). This is an unusual condition scattered in the cladogram. 2. Narrow dark longitudinal line. This is the most common condition in the RTA clade, the dark line corresponds to a compressed internal apodeme (fig. 2B, C). 3. Transverse mark (fig. 3C). Only in *Jacaena* in this dataset. COMMENTS: *Homalonychus*: a slit on a deep pit (scored 12). *Cocalodes*: a slit on a wide depression (scored 02). *Xenoplectus*: fovea lightly sclerotized (scored 2). *Tengella*: intermediate (scored 12).

2. Fovea height relative to cephalon: 0. Fovea as high or lower (fig. 5A–C). 1. Fovea highest (fig. 3G). COMMENTS: *Filistata*, *Pimus*, *Cryptothele*, *Ctenus*, *Toxopsiella*, *Copa*, *Pseudocorinna*, *Agroeca*, *Toxoniella*, *Anagraphis*, *Anyphaena*, *Gayenna*, *Griswoldia*, *Selenops*, *Heteropoda*, *Plexippus*: fovea as high as cephalon (scored 0). *Ciniflella* BRA: about as high as cephalon (scored 0).

3. Carapace flatness: 0. Domed (fig. 5A) or slightly flattened (fig. 4H). 1. Extremely flat, straight drosal profile (figs. 3F, 5D–I). This character was used to group the extremelly flat condition found in some gnaphosoids and in selenopids.

4. Carapace posterior reflexed border: 0. Narrow or not reflexed (fig. 2F, I). 1. Wide reflexed border (fig. 5F). COMMENTS: *Megadictyna*: posterior margin not well sclerotized (scored 0). *Desognaphosa*: very slightly separated (scored 0). *Epidius*: well spaced (scored 1).

5. Large pore-bearing depressions on carapace: 0. Absent (figs. 2I, 9E, 10J). 1. Present (figs. 1C, 3D, 6A, B, D, 7A–C, 6F, G). These may also occur on the sternum (fig. 6C, E).

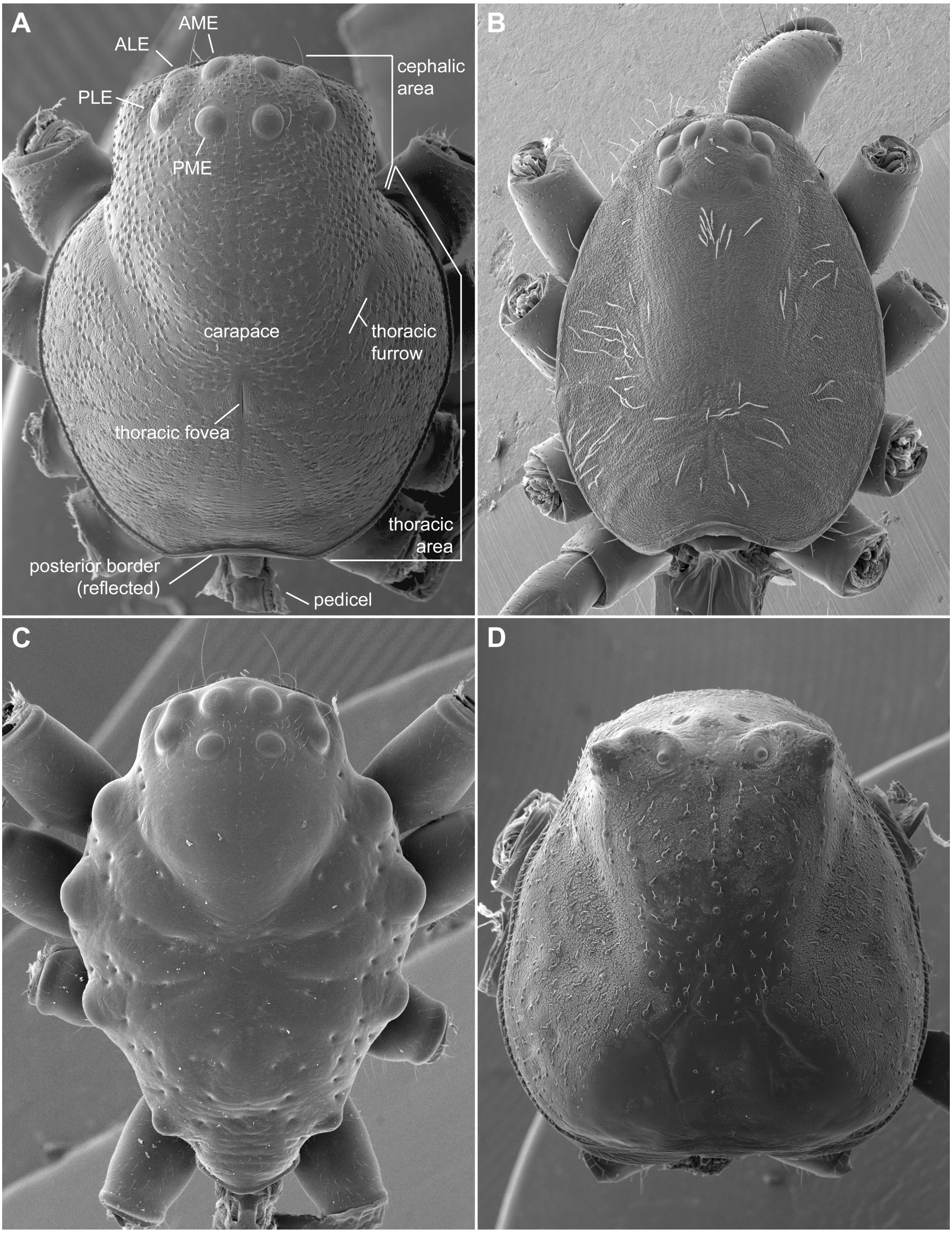

A
AME
ALE
PLE
PME
cephalic area
carapace
thoracic furrow
thoracic fovea
thoracic area
posterior border (reflected)
pedicel
B
C
D

Fig. 1. Female carapace, dorsal view. **A.** *Pronophaea proxima* (Corinnidae). **B.** *Prodidomus redikorzevi* (Prodidomidae). **C.** *Teutamus* sp. (Liocranidae). **D.** *Thomisus onustus* (Thomisidae).

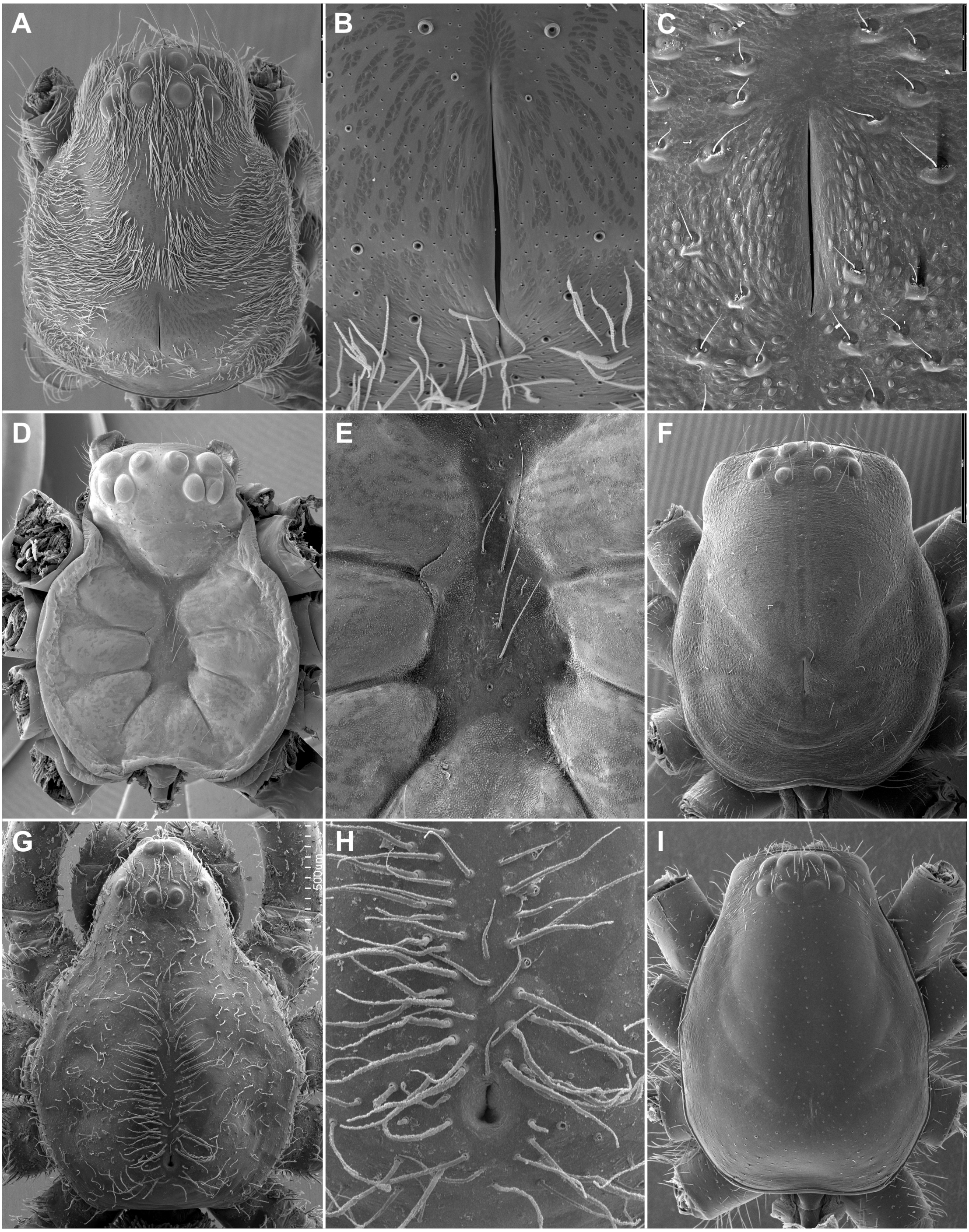


Fig. 2. Carapace and thoracic fovea, female (except G, H immature). **A.** *Paravulsor* sp. (Miturgidae). **B.** Same, thoracic fovea. **C.** *Pronophaea proxima* (Corinnidae), thoracic fovea. **D.** *Hypochilus pococki* (Hypochilidae). **E.** Same, thoracic fovea. **F.** *Falconina gracilis* (Corinnidae). **G.** *Cryptothele alluaudi* (Zodariidae). **H.** Same, thoracic fovea. **I.** *Camillina calel* (Gnaphosidae).

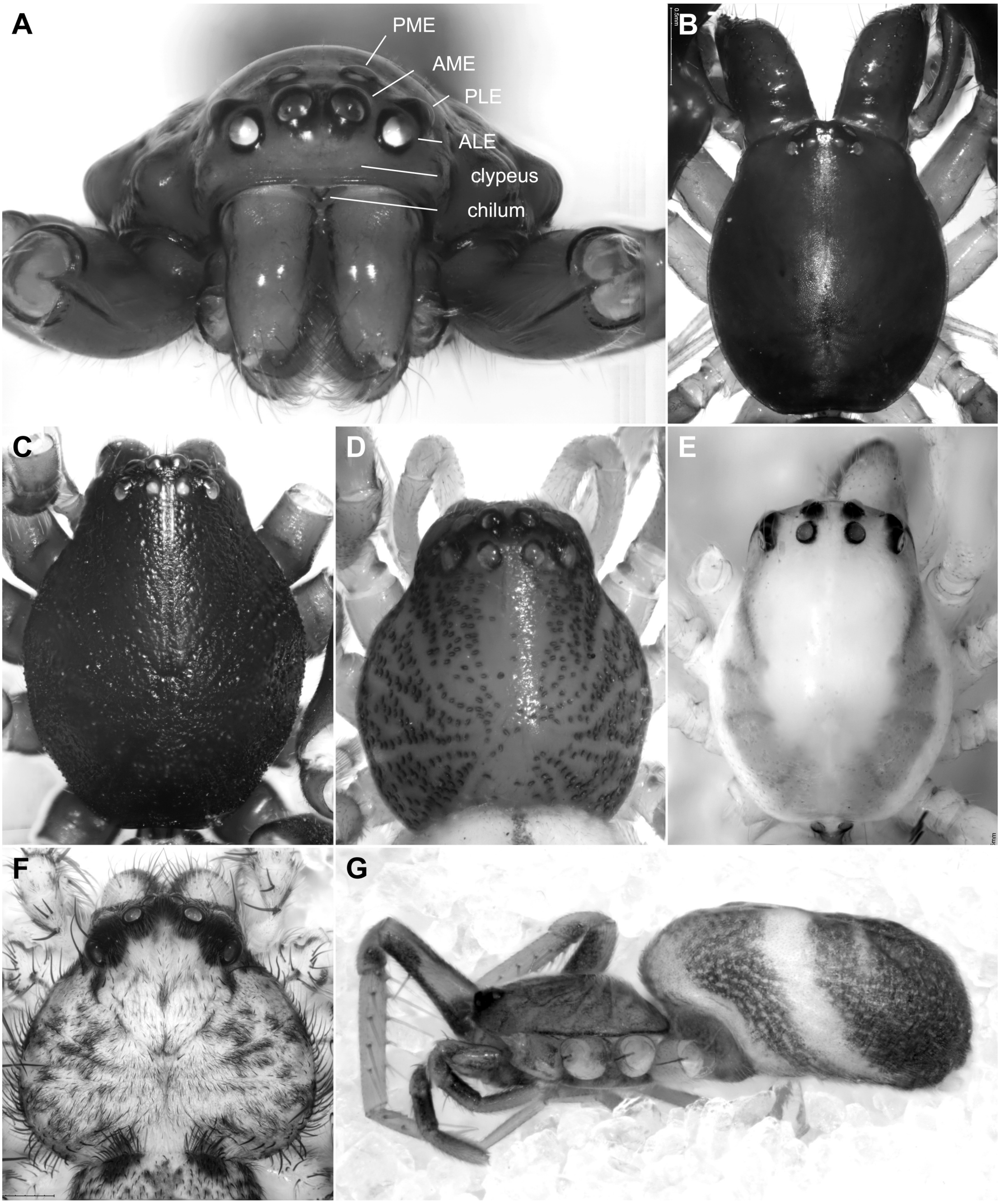

A
PME
AME
PLE
ALE
clypeus
chilum
B
0.5mm
C
D
E
F
G

Fig. 3. Carapace of female (except B, male). **A.** *Teutamus* sp. (Liocranidae). **B.** *Legendrena perinet* (Gallieniellidae). **C.** *Jacaena* sp. (Liocranidae). **D.** Trachelidae ARG. **E.** Eutichuridae MAD (Eutichuridae). **F.** *Anyphops barbertonensis* (Selenopidae). **G.** *Phrurolithus festivus* (Phrurolithidae), habitus lateral.

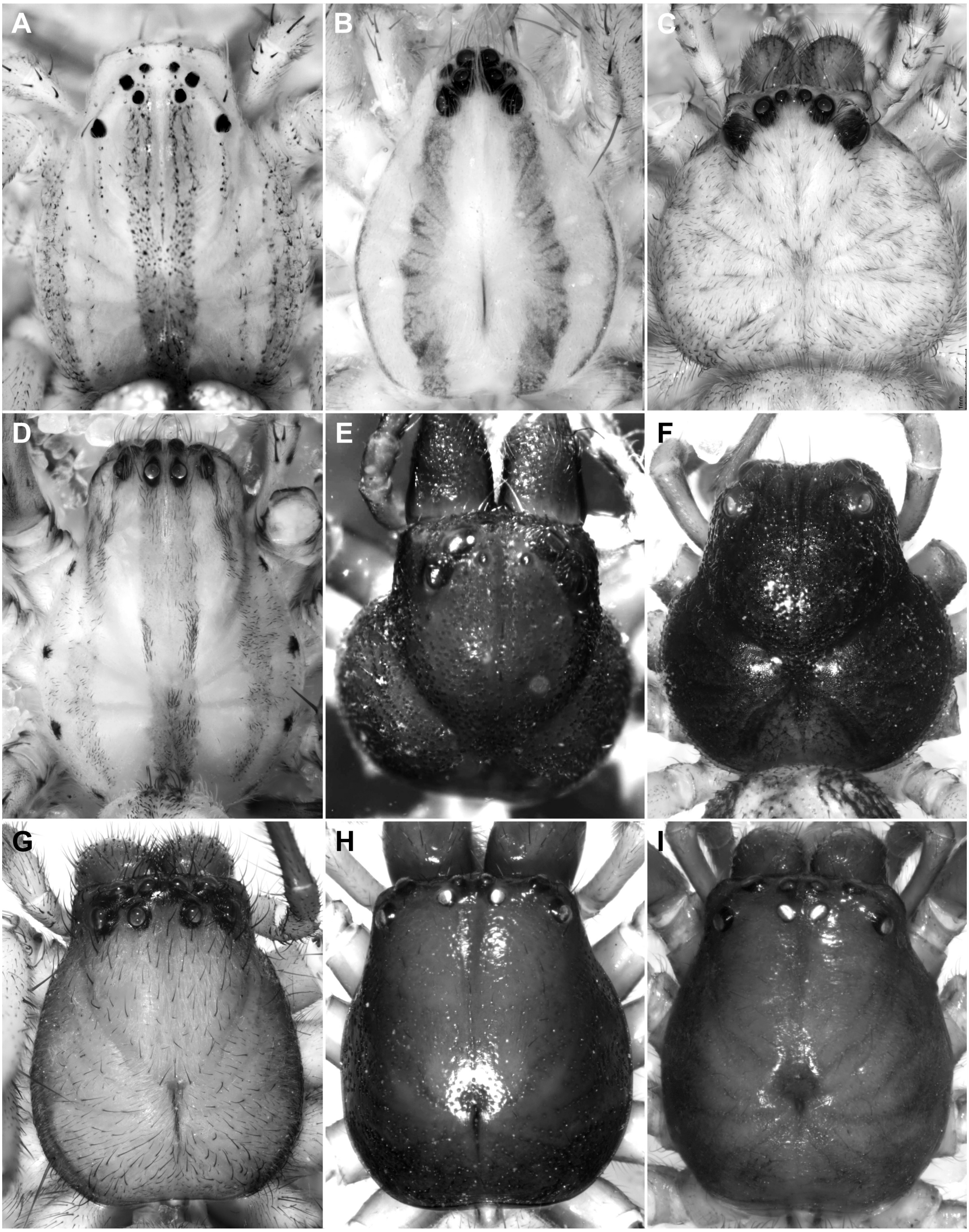


Fig. 4. Carapace of female (except F, male). **A.** *Tibellus oblongus* (Philodromidae). **B.** *Zora spinimana* (Miturgidae). **C.** *Selenops debilis* (Selenopidae). **D.** *Pseudoctenus thaleri* (Zoropsidae). **E, F.** *Cebrenninus rugosus* (Thomisidae). **G.** *Fissarena castanea* (Trochanteriidae). **H.** *Desognaphosa yabbra* (Trochanteriidae). **I.** *Trachycosmus sculptilis* (Trochanteriidae).

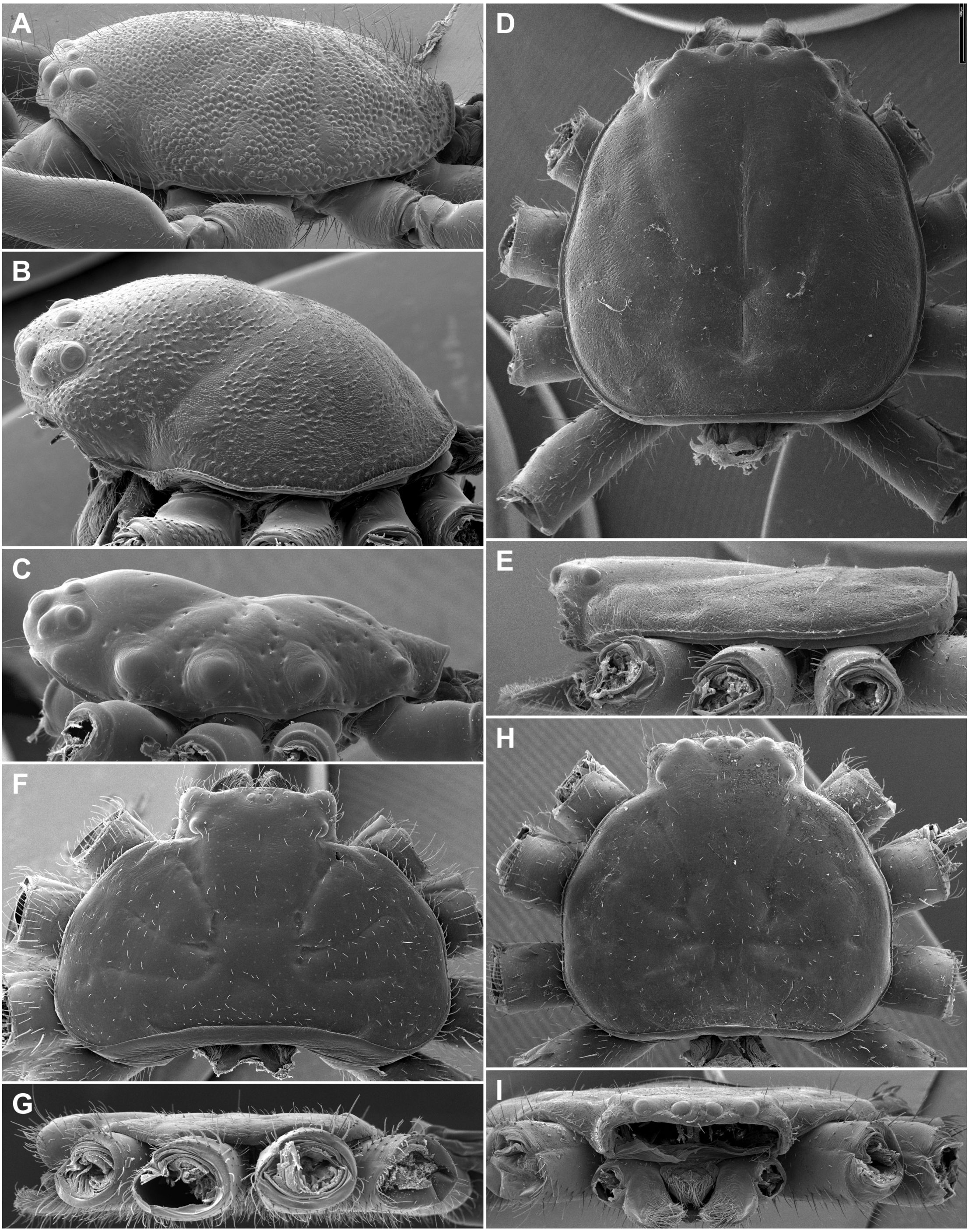


Fig. 5. Carapace of female. **A.** *Sesieutes* sp. (Liocranidae), lateral. **B.** *Pronophaea proxima* (Corinnidae), lateral. **C.** *Teutamus* sp. (Liocranidae), lateral. **D.** *Platyoides walteri* (Trochanteriidae), dorsal. **E.** Same, lateral. **F.** *Vectius niger* (Gnaphosidae), dorsal. **G.** Same, lateral. **H.** *Doliomalus cimicoides* (Trochanteriidae), dorsal. **I.** Same, anterior.

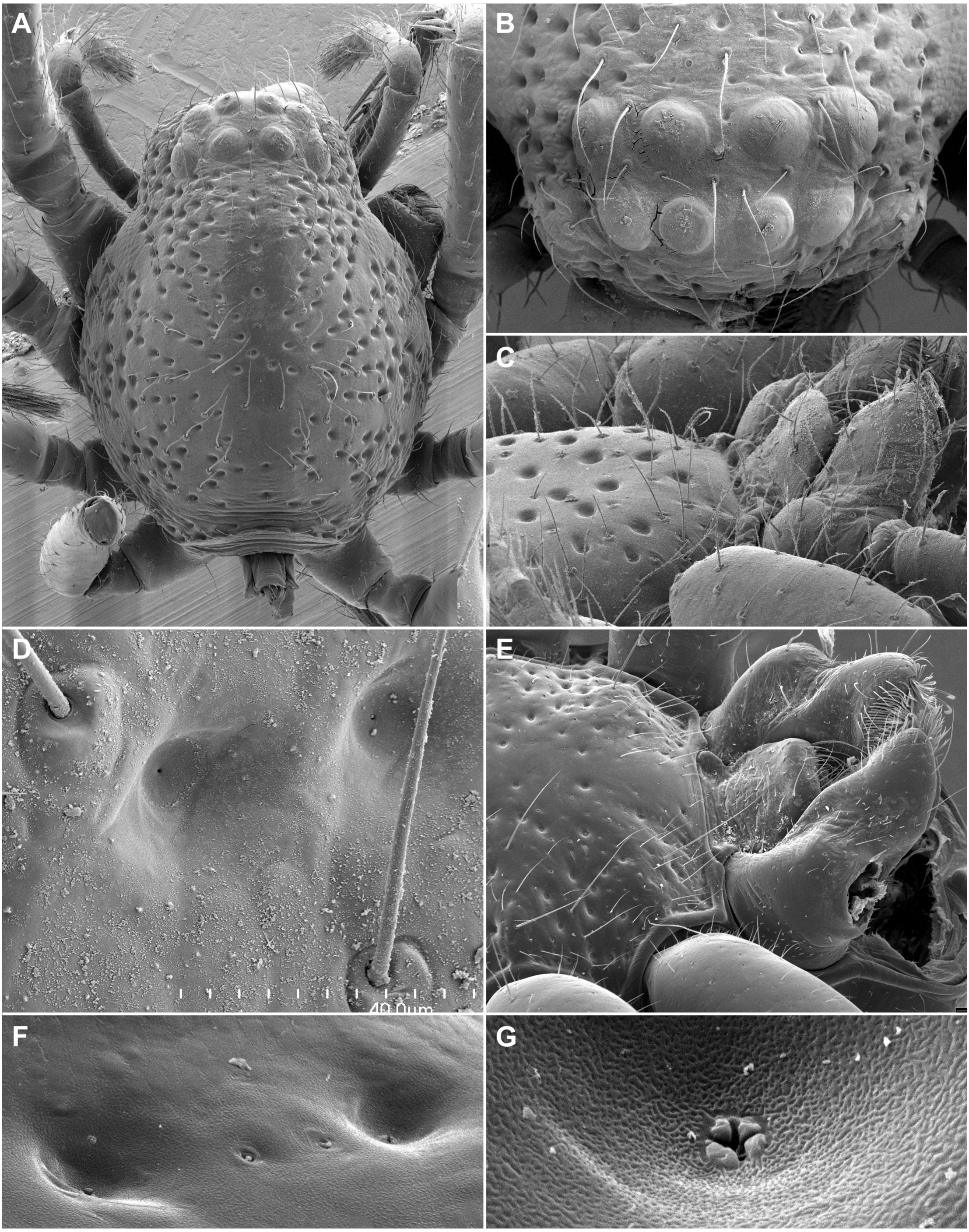


Fig. 6. Structures of cephalothorax, female. **A.** *Orthobula calceata* (Phrurolithidae) carapace dorsal **B.** Same, eyes. **C.** Same, sternum and mouthparts. **D.** Same, detail of pores on carapace. **E.** *Teutamus* sp. (Liocranidae) female sternum and mouthparts. **F.** Same, detail of pores on carapace. **G.** Same, close-up.

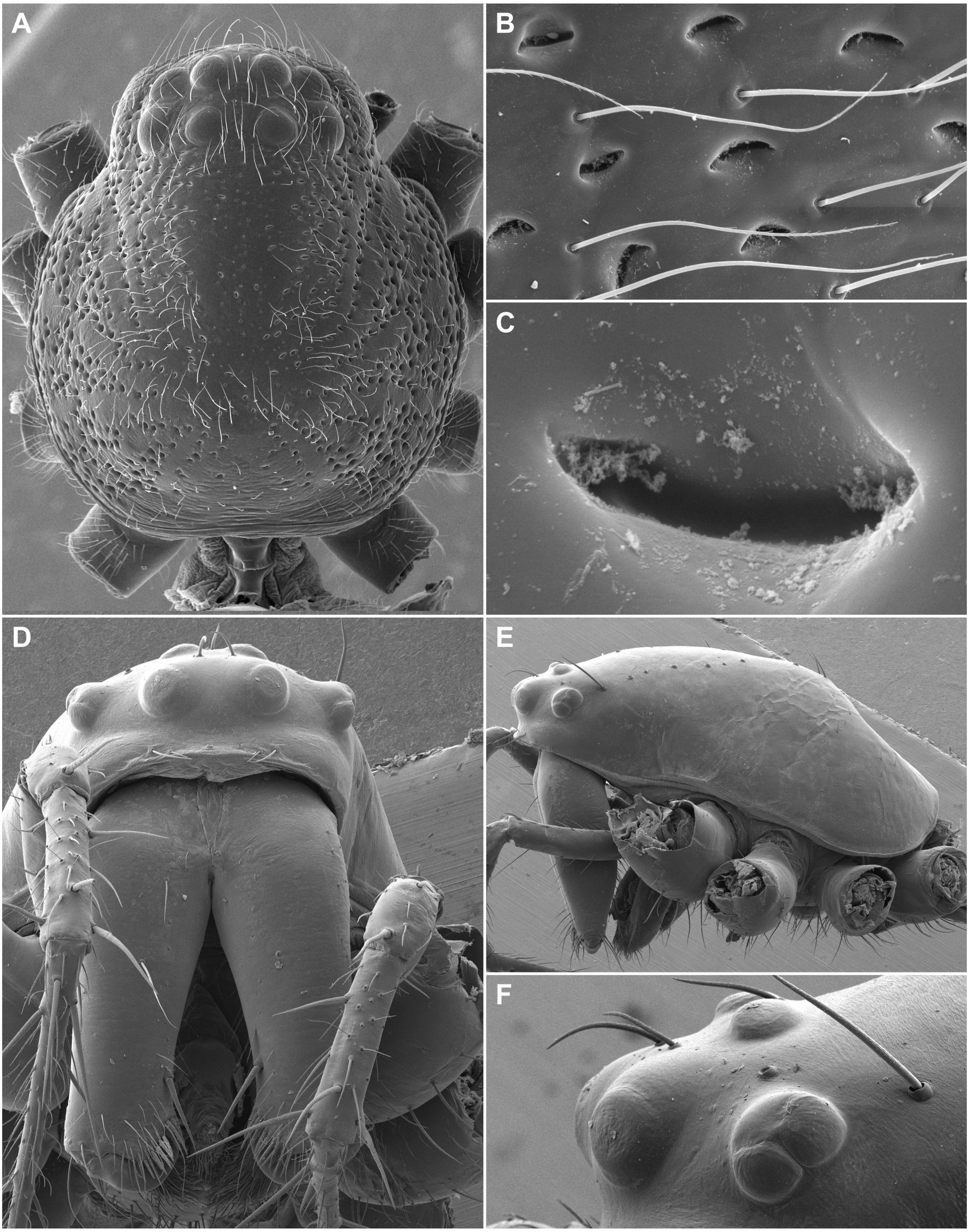


Fig. 7. Structures of carapace, female. **A.** Trachelidae ARG female **B.** Same, detail of pores on carapace. **C.** Same, close-up of a pore. **D.** *Mimetus hesperus* (Mimetidae) female, cephalothorax anterior. **E.** Same, lateral. **F.** Same, eyes lateral.

The depressions have a gland outlet (fig. 6D, F, G). COMMENTS: *Pronophaea*: hair sockets proximally raised and then depressed (scored 0). Trachelidae ARG: elongate depressions (scored 1). *Jacaena:* shallow depressions, scored ambiguous until the presence of pores is tested with SEM (scored 01).

EYES

Spiders have a basic pattern of eight eyes in two rows, and the individual eyes are named relative to this arrangement: anterior median (AME), anterior lateral (ALE), posterior median (PME) and posterior lateral (PME) eyes (figs. 1A, 3A). Each eye is composed of a cuticular lens covering a cellular vitreous body and a retina. All the internal elements are included in an eye cup, or cone, with layer of black pigment. The optical nerve emerges about the distal end of the eye cup. The anterior median eyes are direct eyes, whereby the retina receives the light directly, and the rhabdomers are in front of the nuclei of the photoreceptor cells. In contrast, all other eyes are indirect, with the rhabdomers behind the nuclei, and the light is usually reflected back by a tapetum.

6. ALE-PLE tubercle: 0. Absent, lenses arising on a flat or slightly elevated area (most terminals, fig. 8A), or only the ALE protruding (*Hypochilus*, fig. 8B). 1. Present, both eyes arising from a common tubercle (figs. 3E, 7D, 8D, 12D). This character was suggested by Bonaldo (1994) as a synapomorphy for Eutichurinae. COMMENTS: *Teutamus*: shallow tubercle (scored 0).

7. Lateral eyes on individual bulbous tubercles: 0. ALE and PLE not raised from carapace, or in a common tubercle, not bulbous (fig. 8E). 1. ALE and PLE each on a bulbous tubercle, containing the large eye globes in some higher thomisids (fig. 8F). COMMENTS: *Cebrenninus*: might be intermediate (scored 0). *Strophius*: mostly the PLE (scored 1).

8. ALE-PLE lenses distance: 0. Separated (figs. 9B, D, 10G). 1. Juxtaposed. A classical araneoid character, used here in a very restricted sense, where the limits of the lenses are very close (figs. 7F, 8D).

9. Anterior eye row curvature, in anterior view: 0. Notably procurved (fig. 13A, C). 1. Approximately straight (fig. 14F, G). 2. Notably recurved (fig. 14H, J). States are ordered. Only the more extreme conditions of this continuously varying character are recognized as separate states, with somewhat arbitrary limits. COMMENTS: *Aglaoctenus*, *Homalonychus*, *Macrobunus*, *Medmassa*, *Phrurotimpus*, *Storenomorpha*, *Falconina*, *Pronophaea*, Trachelidae ARG, *Teutamus*, *Camillina*, *Eilica*, *Apodrassodes*: procurved (scored 1). *Cebrenninus*, Miturgidae QLD, *Plexippus*, *Stephanopis ditissima*, *Tibellus*, *Odo bruchi*, *Titanebo*, *Stephanopoides*, *Boliscus*, *Thomisus*: Recurved (scored 1). *Cyrioctea*: slightly procurved. Cf. Liocranidae LIB, *Eusparassus*: slightly recurved (scored 1).

10. Posterior eye row curvature, in dorsal view: 0. Notably procurved (figs. 10G, I). 1. Approximately straight or slightly curved (fig. 4G, H). 2. Notably recurved (fig. 4A, B). States are ordered. Same as preceding. COMMENTS: *Cryptothele*, *Copa*, *Medmassa*: procurved (scored 1). Cf. Liocranidae LIB, *Pseudoctenus*: slightly procurved (fig. 4D) (scored 1). *Teutamus*: about straight (scored 1). *Storenomorpha*, *Trachelas mexicanus*, *Falconina*, *Pronophaea*, *Xenoplectus*, *Gnaphosa*, *Camillina*, *Apodrassodes*, *Lamponella*, *Mituliodon*, *Syspira*, *Selenops*, *Hovops*, *Stephanopis ditissima*, *Borboropactus*: recurved (scored 1). *Eusparassus*, *Eilica*: slightly recurved (scored 1). *Vectius*, *Doliomalus*, *Platyoides*, Eutichuridae MAD, *Paravulsor*, *Ciniflella* ARG, *Titanebo*, *Stephanopoides*, *Boliscus*, *Thomisus*: recurved (scored 1).

11. AME: 0. Present (fig. 9A). 1. Absent (fig. 8C). Losses of direct eyes are represented in this dataset by *Ariadna* and *Lygromma*.

12. AME retina darkness: 0. Present (all terminals). 1. Absent. This character was included to test Jocqué's (1991: char. 11) proposal that Storenomorphinae are grouped by having pale AME. *Storenomorpha* and all other terminals examined here have a dark retina in the direct eyes. COMMENTS: *Apostenus*: this and all data on tapeta scored from drawings by Darrell Ubick (in litt.). Cf. *Moreno* ARG: AME oval. *Cebrenninus*: very small AME, retina on median side.

13. AME cone movable: 0. Immovable. Never reported to my knowledge. 1. Movable. Reported for salticids (e.g., Land, 1969) and thomisids (only observed in *Xysticus* in

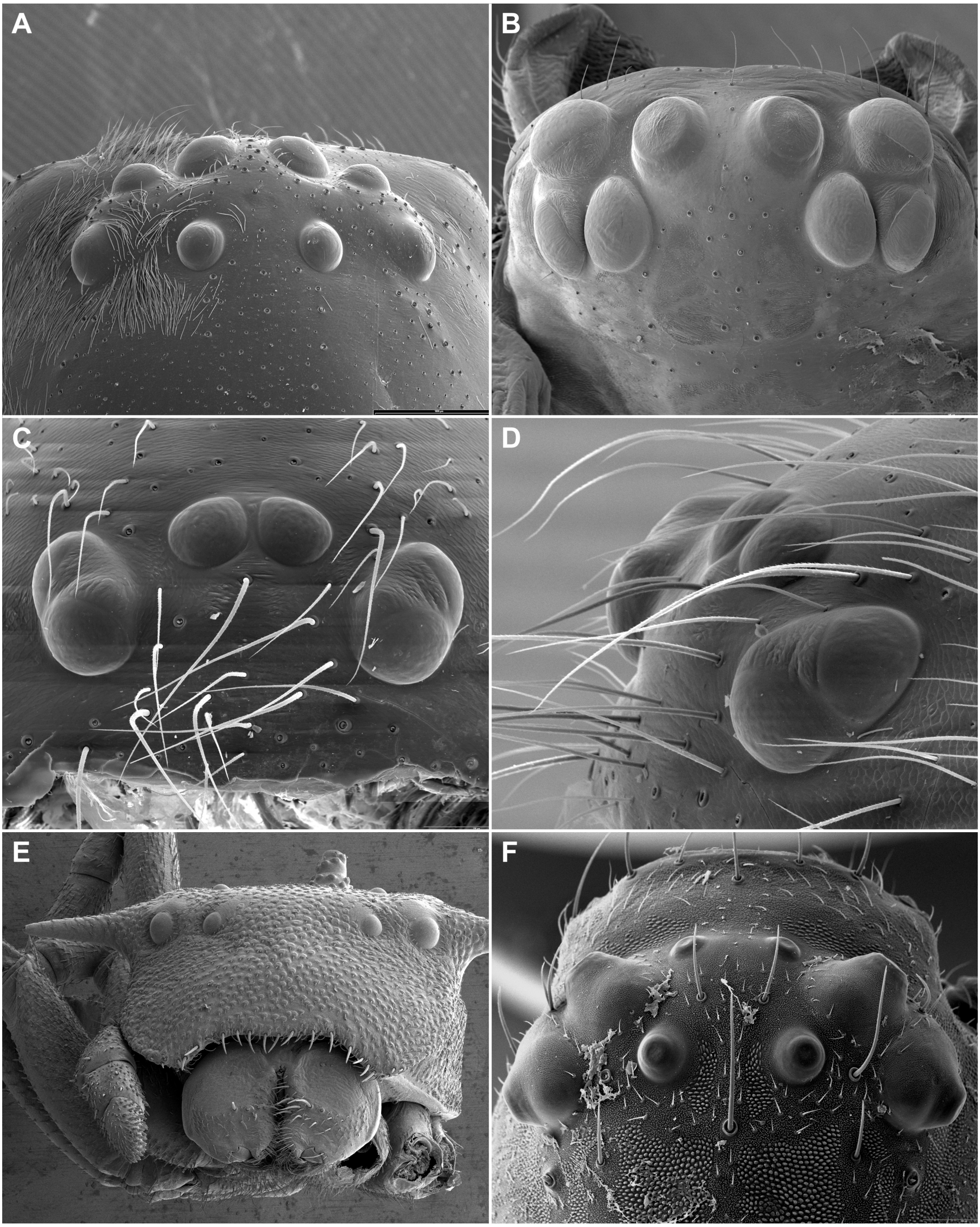


Fig. 8. Eyes of female. **A.** *Eusparassus* cf. *walckenaeri* (Sparassidae), dorsal. **B.** *Hypochilus pococki* (Hypochilidae), dorsal. **C.** *Ariadna boesenbergi* (Segestriidae), dorsal. **D.** Same, lateral. **E.** *Aphantochilus rogersi* (Thomisidae), anterior. **F.** *Tmarus holmbergi* (Thomisidae), dorsal.

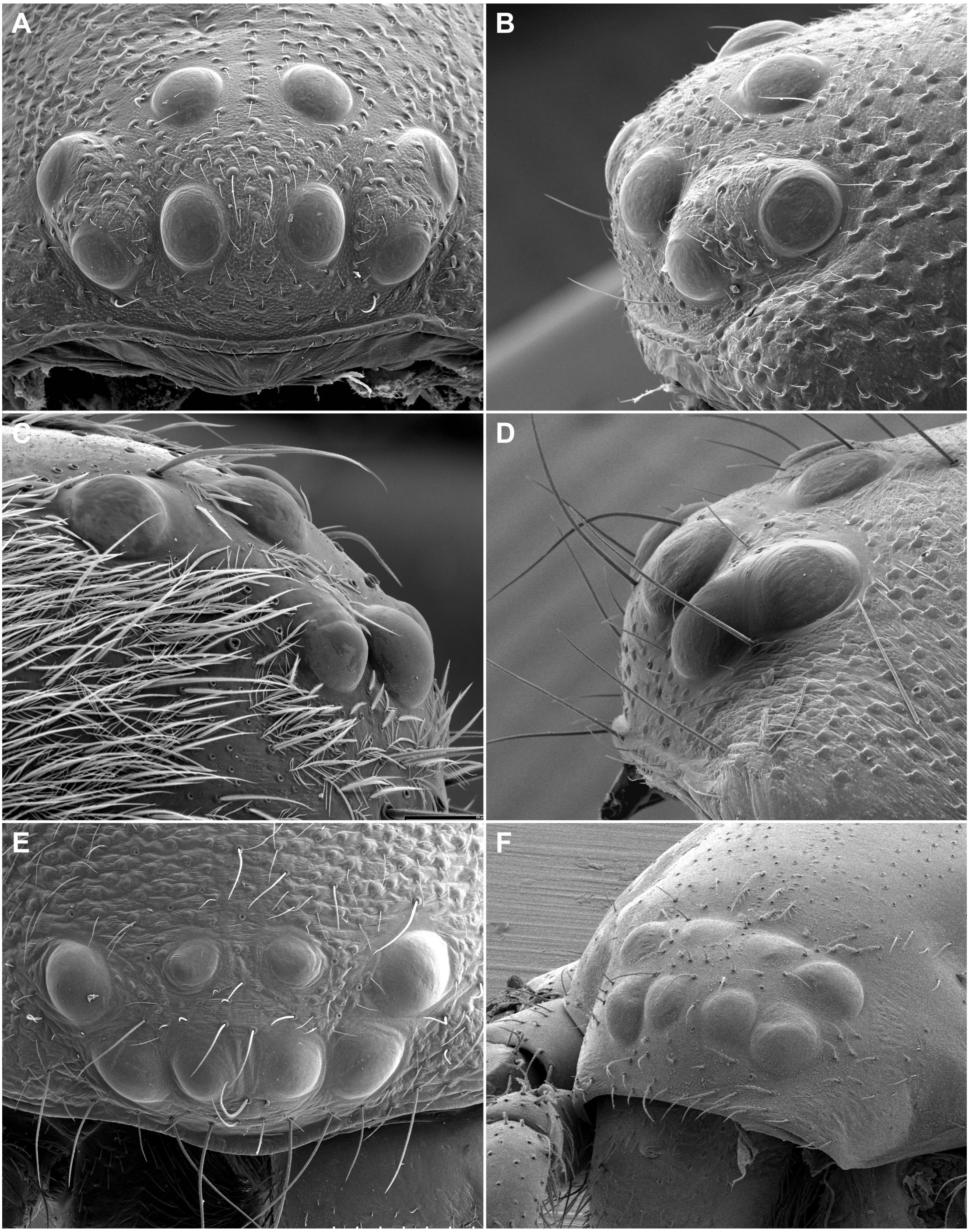


Fig. 9. Eyes of female. **A.** *Pronophaea proxima* (Corinnidae), anterior. **B.** Same, lateral. **C.** *Odo bruchi* (Miturgidae), lateral. **D.** *Falconina gracilis* (Corinnidae), lateral. **E.** *Sesieutes* sp. (Liocranidae), dorsal. **F.** *Phrurotimpus alarius* (Phrurolithidae), anterior-lateral.

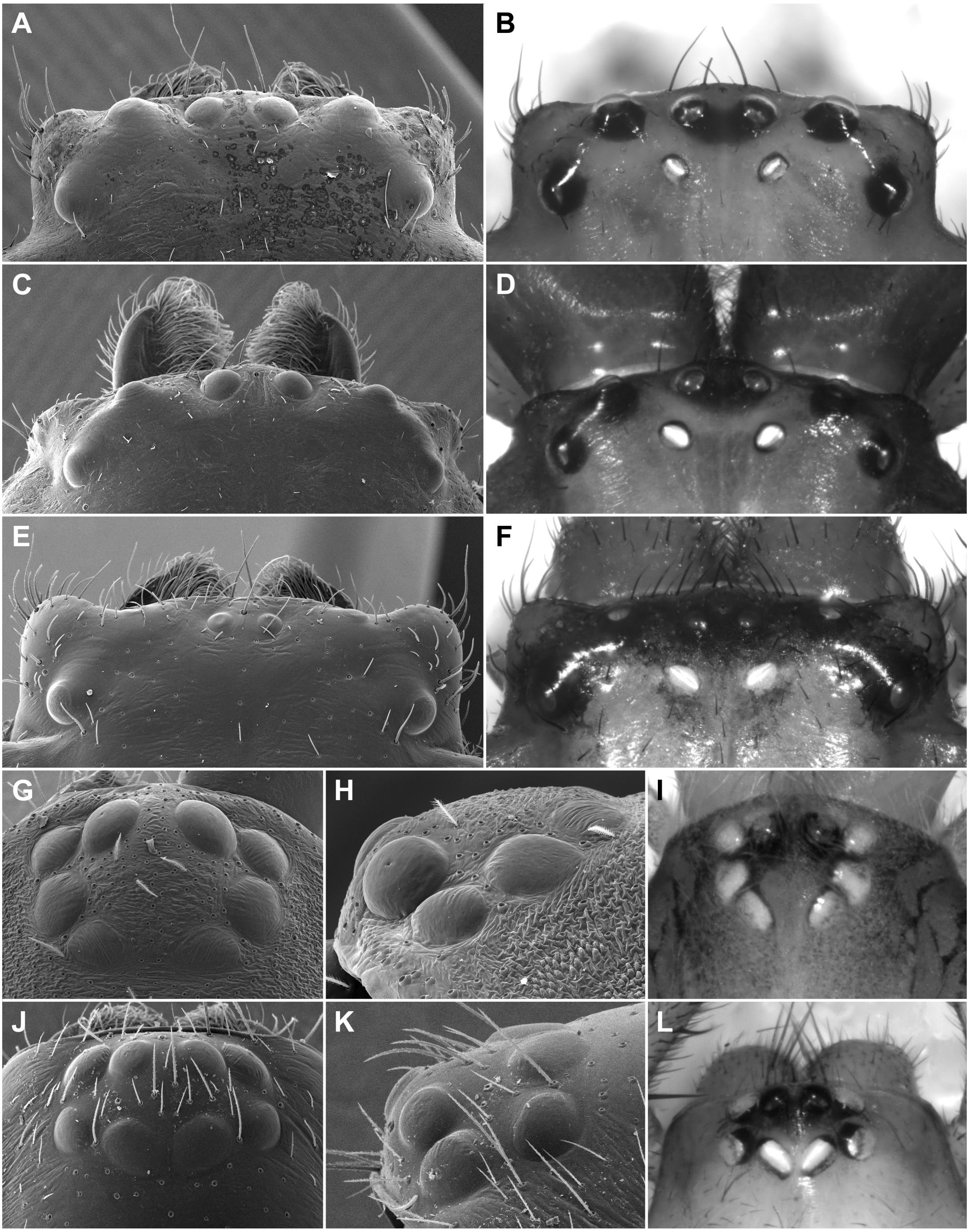


Fig. 10. Eyes of female. **A.** *Doliomalus cimicoides* (Trochanteriidae), dorsal, SEM. **B.** Same, light microscopy. **C.** *Platyoides walteri* (Trochanteriidae), dorsal, SEM. **D.** Same, light microscopy. **E.** *Vectius niger* (Gnaphosidae), dorsal, SEM. **F.** Same, light microscopy. **G.** *Prodidomus redikorzevi* (Prodidomidae), dorsal, SEM. **H.** Same, lateral. **I.** Same, dorsal, light microscopy. **J.** *Camillina calel* (Gnaphosidae), dorsal, SEM. **K.** Same, lateral. **L.** Same, dorsal, light microscopy.

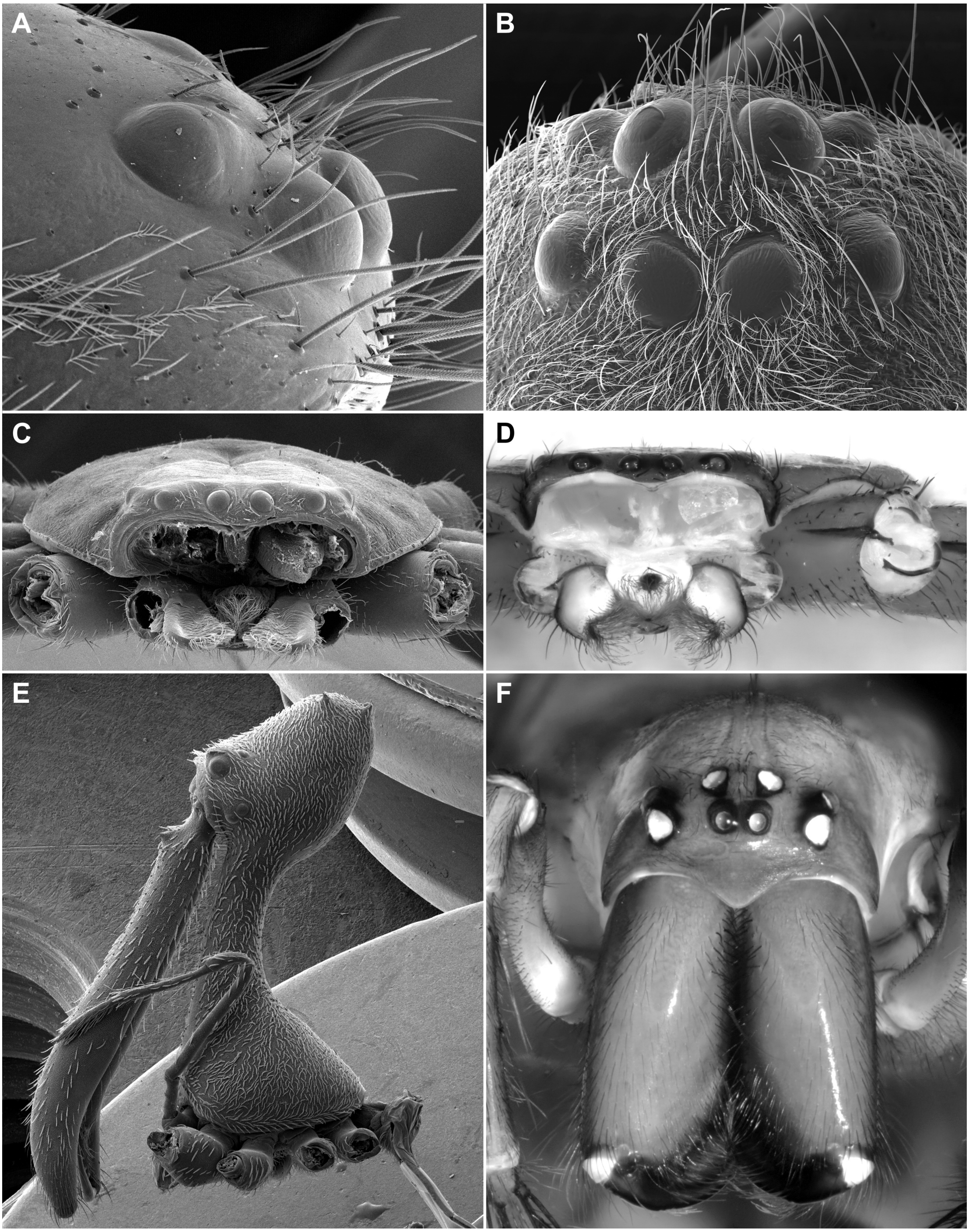


Fig. 11. Cephalothorax and eyes, female. **A.** *Apodrassodes quilpuensis* (Gnaphosidae), eyes lateral. **B.** *Lampona cylindrata* (Lamponidae), eyes dorsal. **C.** *Platyoides walteri* (Trochanteriidae), anterior. **D.** *Doliomalus cimicoides* (Trochanteriidae), anterior. **E.** *Eriauchenius workmani* (Archaeidae), lateral. **F.** *Hickmania troglodytes* (Austrochilidae), anterior.

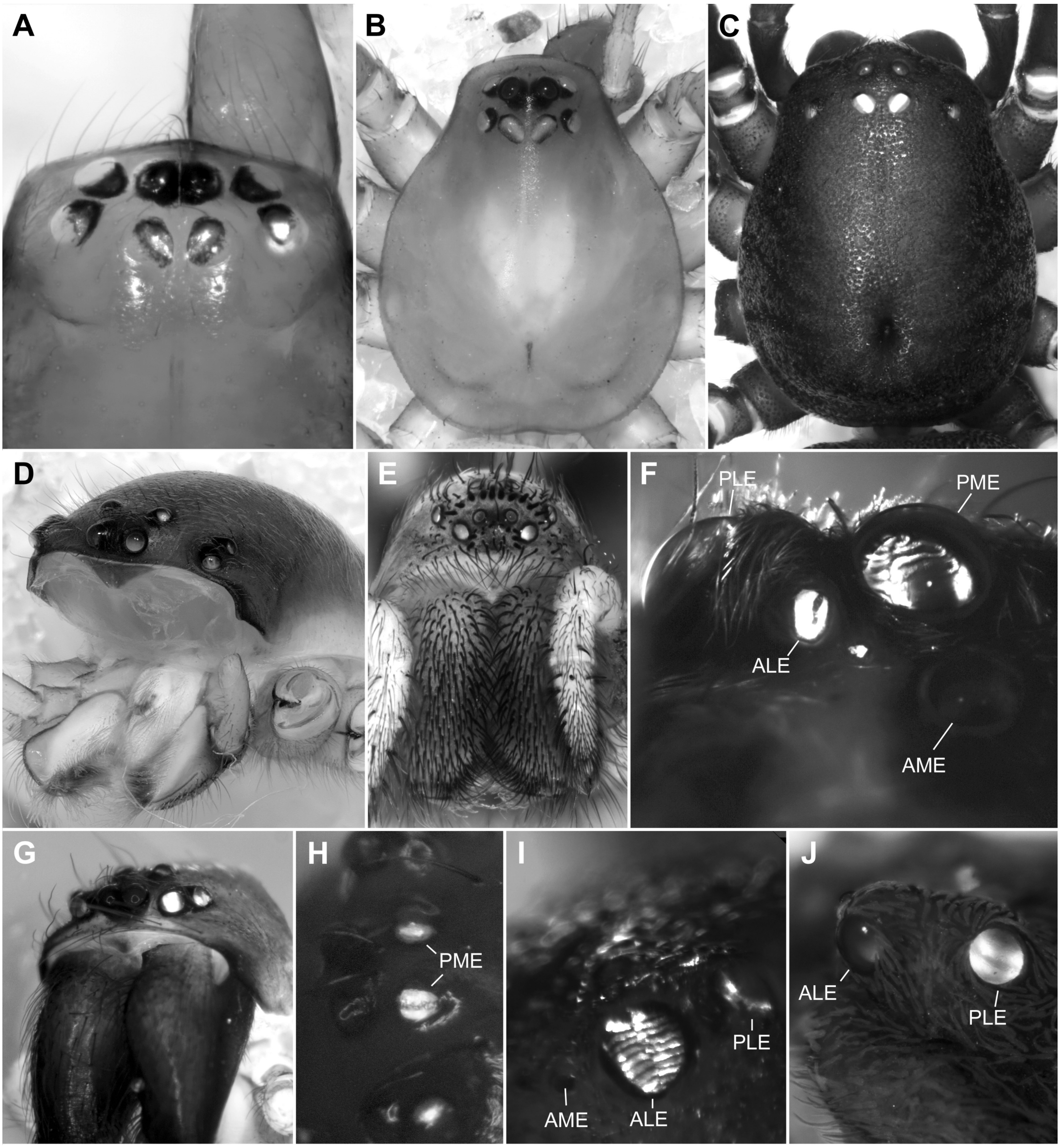


Fig. 12. Carapace, eyes and tapeta, female (except F–G, male). **A.** *Pseudolampona emmett* (Lamponidae). **B.** *Cithaeron delimbatus* (Cithaeronidae). **C.** *Asadipus kunderang* (Lamponidae). **D.** *Macerio flavus* (Eutichuridae) anterior-lateral. **E.** *Cyrioctea spinifera* (Zodariidae) anterior. **F.** *Acanthoctenus* sp. from Calilegua (Ctenidae), shining tapeta of PME (large) and ALE (small). **G.** *Amaurobius similis* (Amaurobiidae). **H.** *Nicodamus mainae* (Nicodamidae) shining tapeta of PME. **I.** *Cebrenninus rugosus* (Thomisidae) shining tapeta of ALE. **J.** *Borboropactus bituberculatus* (Thomisidae) shining tapetum of PLE.

this dataset). It has been suggested that movable AME may be a synapomorphy joining Thomisidae with Salticidae, two families with excellent visual systems (W. Maddison, oral presentation during the XVI International Congress of Arachnology and personal commun.). The internal movement of the large AME of salticids can be easily

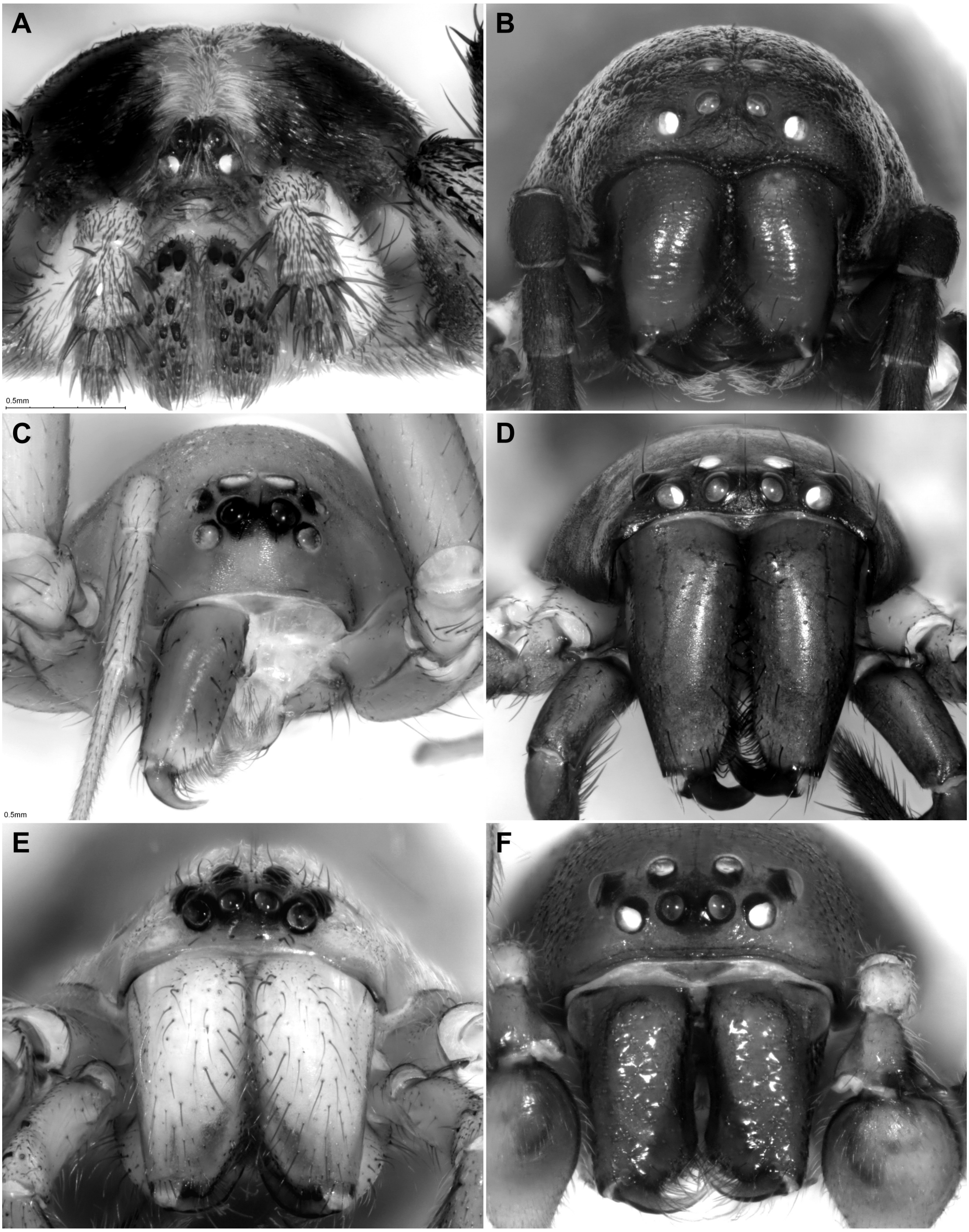


Fig. 13. Cephalothorax anterior, female (except F, male). **A.** *Ammoxenus amphalodes* (Ammoxenidae). **B.** *Asadipus kunderang* (Lamponidae). **C.** *Cithaeron delimbatus* (Cithaeronidae). **D.** *Galianoella leucostigma* (Gallieniellidae). **E.** *Agroeca brunnea* ("Liocranidae"). **F.** *Meriola barrosi* (Trachelidae).

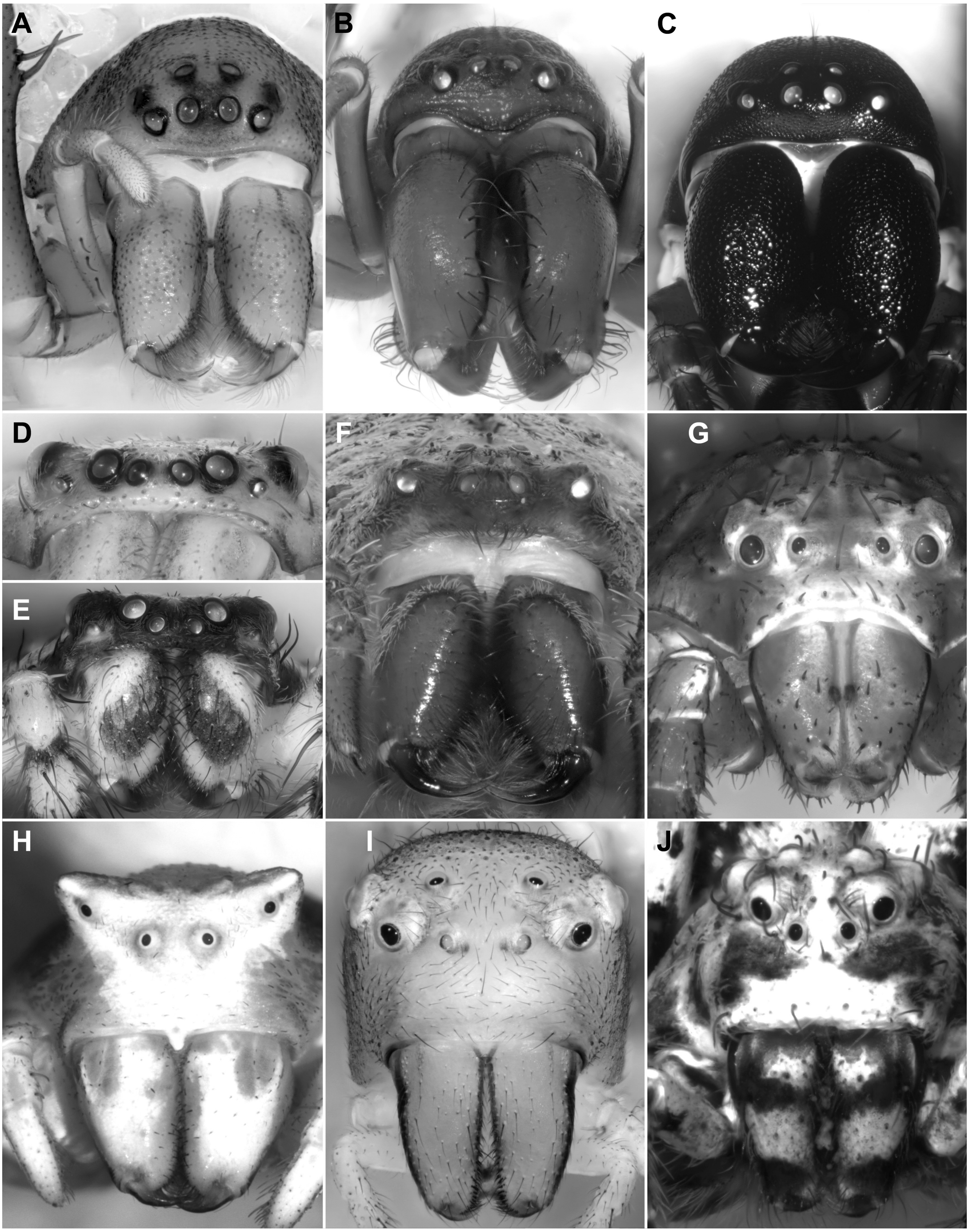


Fig. 14. Cephalothorax, anterior. **A.** *Pronophaea proxima* (Corinnidae) female. **B.** *Oedignatha* sp. (Liocranidae) male. **C.** *Corinna nitens* (Corinnidae) female. **D.** *Selenops debilis* (Selenopidae) male. **E.** *Anyphops barbertonensis* (Selenopidae) female. **F.** *Borboropactus bituberculatus* (Thomisidae) female. **G.** *Strophius albofasciatus* (Thomisidae) female. **H.** *Thomisus onustus* (Thomisidae) female. **I.** *Alcimochthes limbatus* (Thomisidae) female. **J.** *Petrichus* sp. (Philodromidae) female.

seen with the naked eye, but there are no negative reports for other spiders with smaller AME. The anatomy suggests that all spiders can move the AME cone to some extent, as Homann (1971: 208) described that in the AME of spiders in general: "One to six muscles can pull the retina to the side, increasing the field of vision." COMMENTS: *Xysticus*: scored from *Xysticus* sp., NY, Centereach (V. Ovtsharenko) OMA movable. *Stephanopoides*: muscles observed in subadult female, dissected, MJR-1319 (scored ?).

14. AME cone length: 0. Short cone or sphere (Homann, 1971: fig. 1A, B). 1. Long cone; unique to Salticidae (Homann, 1971: fig. 1C; Land, 1969; Blest et al., 1990). This character works as a proxy for the complex visual system and characteristic eye arrangement of salticids. See Blest et al. (1990) and references therein for details of the salticid retina, which seem to be informative for relationships within the family.

15. AME-ALE reflection of white light: 0. White reflection, no change in color (figs. 4I, 13D, E, 14G). 1. Color reflection (see color versions of figs. 12F, 14I in Morphbank). A colored reflection on a lens surface illuminated with white is indicative of interference, such of that produced by antireflex coating of lenses. Salticids and some thomisids have such color reflection, which is coherent with an antireflex function associated with high quality vision. Hill (2009: 7) has reported that green reflection on anterior eyes can be observed in many salticids. COMMENTS: *Acanthoctenus*: a freshly killed *Acanthoctenus* sp. from Calilegua had orange reflection in all eyes except ALE (preparation MJR-1318) (scored 01). *Vulsor*, *Ctenus*: only blue-purple reflection on tangent incident axes, seemingly an effect of cuticle sculpture (scored 0). *Senoculus*: only coating in PME, PLE, orange (scored 0). *Teutamus*: All sclerotized surfaces with green reflection, except eye lenses (scored 0). *Lessertina*: yellow, AME (scored 1). *Ciniflella* ARG: almost not reflection (scored ?). *Thomisus*: some specimens reflect pink to purple, especially at the margins of the eyes, not so much at the center (scored 01). *Cocalodes*: yellow (scored 1). *Holcolaetis*: yellow (scored 1). *Hispo*: only AME, green (scored 1). *Plexippus*: AME green, ALE orange (scored 1).

16. ALE black cup: 0. Well developed. The cup of black pigment surrounds the entire optic chamber, so that on external view the eye is dark; there may be a silvery tapetum on top of the dark background of the cup. 1. Cup reduced, ALE pale. The black pigment is irregularly distributed or absent altogether; the eye globe is flattened, seemingly vestigial. In several lycosoids the reduction of the ALE eye cup is concomitant with the reduction and asymmetry of the tapetum. In gnaphosoids, especially prodidomids, the black cup is absent, but the eyes are still large, flattened (see chars. 26 and 28). COMMENTS: *Oecobius*: irregular, white, as flat as the surrounding cuticle (scored 1). *Eriauchenius*: silvery, large tapetum, as well as in PME and PLE (scored 1). *Gayenna*: small but normal (scored 0). Cf. Liocranidae LIB: specimens are faded, badly preserved (scored ?). *Acanthoctenus*: small patch of black pigment superior to eye cup (scored 1). *Vulsor*, *Ctenus*: reduced (scored 1). *Xenoctenus*: pearly, not much black in the cup (scored 1). *Hovops*: black cup present but small (scored 0).

17. PME position relative to anterior eye row: 0. PME well behind AME. 1. PME approximately in line with AME. A characteristic eye arrangement unique of Selenopidae (figs. 4C, 14C, D).

18. PME vestigial: 0. Well developed (fig. 8F). 1. Very small, vestigial. This character was loosely used to distinguish between basal and derived salticids (e.g., Maddison and Hedin, 2003: 543; Wanless, 1987). It also occurs in *Cebrenninus rugosus*, some specimens of which may lack the PME altogether (compare fig. 4E, F).

19. PME lens curvature: 0. Convex (figs. 5C, 9C). 1. Flattened (figs. 9E, F, 10H, J, K, 11A, B, 12B, 13C). This is a classical character of Gnaphosoidea (Platnick, 2002: char. 1; 2000: char. 9). The lack of an image-forming lens seems loosely correlated with the function of the PME as polarized light detectors, with their tapeta axes forming a 90° angle (see char. 26). In some gnaphosoids and in *Oecobius*, the cuticle is totally flat (fig. 10A–F). Platnick (2002: 7) noted that morebiline trochanteriids have domed eyes, but presumed that their eyes might be structurally equivalent to those of gnaphosoids. At least the morebiline *Fissarena*, with domed eyes, lacks the perpendicularly oriented axes of PME tapeta. I found domed lenses scattered among several gnaphosoids, some of which also have the generalized condition of parallel PME tapetum axes. COMMENTS: *Filistata*: elongated, irregular, but not flattened (scored 0). *Nicodamus*: oval, transverse, not flattened (scored 0). Trachelidae ARG: about triangular (scored 01). Cf. Gnaphosoidea TEX: at least not as flat as in prodidomids, quite regularly convex as well (scored 0). Cf. *Moreno* ARG: intermediate (scrored 01). *Lampona*: Flat, oval (scored 1). *Pseudolampona*: slightly domed (scored 0). *Centrothele*: oval, transverse, not flattened, contra Platnick (2000). *Legendrena*: oval, perpendicular to tapetum (scored 1). *Austrachelas*: slightly convex (scored 01). *Desognaphosa*: small, convex PME (scored 0). *Cithaeron*: oval parallel to tapetum (fig. 12B) (scored 1). *Cebrenninus*: when present, round convex (scored 0).

20. PME lens limits: 0. Lens raised from surrounding cuticle (figs. 9C, 10J). 1. Lens not raised, totally flat (fig. 10C, E).

21. ALE tapetum: 0. Present. This is the generalized condition (fig. 12G, I). 1. Absent. The tapetum of indirect eyes has been lost in some spiders with good visual systems (salticids, oxyopids, philodromids), but also in other groups without any indication of visual specializations (eresids, uloborids). Although the loss of the tapeta commonly occurs coordinately in all the posterior eyes, there are several exceptions; hence, the tapetum is scored as independent characters for each eye. In this dataset *Anyphops* (Selenopidae) and the cycloctenids *Cycloctenus* and *Toxopsiella* have a tapetum in ALE but not in PME-PLE; in the three cases the ALE tapetum is vestigial. So far all known spiders without a tapetum in ALE also lack it in the posterior eyes. In the indirect eyes of spiders, the retinal cells have the rhabdomes immediately external to the tapetum, while a part of the cell, including the nucleus, is placed more distally, between the tapetum and the vitreous body plus lens (Homann, 1971). The retinal cells form externally in ontogeny; later their extensions cross the tapetum to meet the nerves. Eyes with a tapetum are also called nocturnal eyes, although there seems to be no experimental evidence of adaptation to dim light (Foelix, 2011). COMMENTS: *Senoculus*: there is no black pigment cup (scored ?). *Neato*: tapetum from female in clove oil, median line of the canoe not visible, but axis evident (scored 0). *Ammoxenus*: tapeta from *A. amphalodes* (scored 0). *Lamponella*: tapetum visible in female QMS67147 (scored 0). Cf. Eutichuridae QLD: specimens not well preserved, not visible under lactic acid (scored ?). *Syspira*: specimens boiled, opaque; tapetum scored from another species from Dominican Republic, which has canoe tapeta: ALE vertical, PLE horizontal, PME parallel (scored 0). *Ciniflella* ARG: tapeta observed in two living specimens, schemas with specimens (scored 0). *Ciniflella* BRA: All specimens badly preserved, several cleared in clove oil; I saw some faint middle lines, but the observations are not good. The general shape of the tapeta is more consistent with canoe than with grate. Other similar species seemed to have canoe tapeta in all eyes as well (scored 0). *Boliscus*: specimen clarified in clove oil, cuticular iris is too small to see tapetum (scored ?). *Thomisus*: In the dissection the black cup was filling a large part of the eye ball, the iris is very small, and the tapetum was barely visible. A broken PME showed a grate tapetum (scored 0). *Petrichus*: dissected, clove oil, there are multiple round orifices as in AME, no tapetum (scored 1). *Holcolaetis*: eyes dissected, cleared in clove oil, no tapetum (scored 1). *Portia, Lyssomanes*: eye anatomy well studied (see references in Blest et al., 1990) (scored 1).

22. ALE tapetum type: 0. Primitive. The retinal cells pass through the tapetum through several holes arranged in a medial line (Homann, 1971). 1. Canoe. The retinal cells pass through a definite, continuous slit instead of several holes, and the rhabdomes are platelike, perpendicular to the median slit (Homann, 1971) (fig. 12F, J). 2. Grate. The slit is folded in a complex shape, reminiscent of a fireplace grate (Homann, 1971) (fig. 12I). 3. Hexagonal pattern of holes uniformly distributed. Typical of Sparassidae (Homann, 1971; Land, 1985; Nørgaard et al., 2008), but not Sparianthinae, which have canoe tapeta. A grate tapetum is usually easy to identify, but the differences between canoe and primitive tapeta are subtler on external examination, clarification, or in gross dissections. There are several inconsistencies between the reports by Homann (1971) and the observations here. In some cases where the tapetum is lost but the retinal rods show signs of organization typical of a grate, the character was scored from the retinal rods (*Oxyopes*) as reported by Homann (1971). The grate-shaped tapetum of at least some lycosids have rods (similar to coffee grains, made by the rhabdomes of two cells) isolated by the pigmentogen, giving the aspect of isolated spots of tapetum (Homann, 1971: cf. fig. 29A–C). Other lycosids lack the isolation of the rods, and the tapetum bands are visible as continuous (Homann, 1971: fig. 29D). COMMENTS: *Oecobius*: Considered primitive by Homann (1971). *O. navus* has a quite sharply defined vertical line on the ALE. Because the tapetum of *Uroctea* combines features of the primitive and canoe-shaped type (Homann, 1971), and the external appearance of a canoe tapetum, it is scored ambiguous (01). *Araneus*: after Homann (1971), although the median line is not well defined; also examined images from Nikolaj Scharff (scored 1). *Eriauchenius*: tapetum type from Homann (1950: 61), but I cannot see any line on any of the indirect eyes (scored ?). *Nicodamus*: median line not well marked (scored 01). *Stiphidion*: from Gray and Smith (2004: 138) (scored 1). *Calacadia*: I cannot see the median line (scored ?). *Storenomorpha*: in all indirect eyes there is a median band of irregular appearence, perhaps many small holes (scored 1). *Psechrus*: note that in *Fecenia*, ALE canoe, the rest grate (Homann, 1971) (scored 2). *Acanthoctenus*: Perhaps just a reduced grate, almost a ring, with central oval dark patch. Homann (1971) identified as canoe. Griswold (1993), citing Homann (1971) and his personal observation, said that the Ctenidae have a great shaped tapetum in "at least two pairs of eyes." Preparation MJR-1318 is closer to a canoe (fig. 12F) (scored 1). *Oxyopes*: no tapetum, but grate disposition of retinal rods (scored 2). *Dolomedes*: grate, but whitish, reduced and irregular (scored 2). *Cycloctenus*: reduced, irregular, with irregular dark spots (scored 012). *Toxopsiella*: reduced; see also Homann (1971) (scored 012). Cf. *Medmassa* THA: all indirect eyes with visible tapetum, but median line not clear (scored 01). *Castianeira*: I cannot see the median line, but not grate shaped (scored 01). *Toxoniella*: ALE and PLE canoe deduced from general shape, line not visible (scored 01). *Neoanagraphis*: median line not seen, only the symmetry (scored 01). *Teutamus*: line not seen, but clearly not grate (scored 01). *Hortipes*: too small to see (scored ?). *Pseudolampona*: all tapetum characters scored after clarification with clove oil, median line of canoe sharply defined (scored 1). Cf. Gnaphosoidea TEX: I cannot see the median line, but not grate shaped (scored 01). *Meedo*: all tapeta very weak, but shiny (scored ?). *Doliomalus*: I cannot see the line (scored 01). *Desognaphosa*: not very clear whether canoe or primitive (scored 01). *Malenella*: after clearing with lactic acid and then back to alcohol, the median line is hard to see and not very thin, but still definite (scored 1). *Eutichurus*, *Cheiramiona*, *Macerio*: a median band with small dark spots (scored 0). Eutichuridae MAD: observed in clove oil (scored 0). *Mituliodon*: grate; see also Griswold (1993), who reported a grate tapetum in ALE, PME, and PLE (scored 2). *Miturga gilva*: widely convoluted, external half without loop (scored 2). *Systaria*: all indirect eyes very shiny, giving the gnaphosoid appearance; all with a median wide band of dark dots (scored 0). *Uliodon*: C-shaped, externally convex (scored 12). *Liocranoides*: all tapeta with a band of dark spots like in eutichurids (scored 0). *Selenops*: a reduced tapetum like those of the ctenids; identified as canoe by Corronca (1997) (scored 012). *Anyphops*: a plate perforated by many dark holes in a vertical band (scored 0). *Heteropoda*: the small dark holes are regularly spaced in hexagonal pattern (scored 3). *Polybetes*: a large plate perforated by many small dark holes, symmetry axis not evident (scored 3).

23. ALE tapetum symmetry axis: 0. Vertical (fig. 12F) or oblique down to external (fig. 12I). 1. Horizontal (fig. 12J). COMMENTS: *Araneus*: male vertical, female oblique (scored 0). *Eriauchenius*: no line visible (scored ?). *Zoropsis*: heart shaped, two anterior arms and median line horizontal (scored ?). *Vulsor*: sinuous, irregular (scored 0). *Ctenus*: irregular line (scored 0). *Xeno-*

plectus: variable, one male clearly horizontal, another clearly oblique (scored 01). *Prodidomus, Neozimiris*: oblique, which is also parallel to PME and 90° with PLE, seemingly part of the polarized light detector (scored 0). *Lampona*: sinuous canoe line (scored 1). *Ammoxenus*: oblique in *Ammoxenus* cf. *coccineus*, vertical in *A. amphalodes* (scored 0). *Doliomalus*: extended horizontally, but I cannot see the line (scored ?). *Miturga* cf. *lineata*: irregular loops (scored ?). *Mituliodon,* Miturgidae QLD: irregular (scored ?). *Paravulsor*: close to horizontal (scored 01). *Griswoldia*: the symmetry axis is horizontal, contorted, the grate tapetum looks irregularly folded (scored 1). *Selenops*: a reduced tapetum like those of the ctenids (scored 0). *Hovops*: a reduced tapetum like those of the ctenids (scored 0). Sparianthinae VEN: tapeta from male penultimate (scored 1). *Borboropactus*: horizontal, sinuous (scored 1).

24. PME tapetum: 0. Present. 1. Absent. COMMENTS: *Selenops*: in a key to families, Homann (1951: 141) says that the posterior eyes of Selenopidae (he examined *Selenops*) lack tapetum. Later Homann (1971) reported a reduced tapetum with resemblances with those of Sparassidae and Cycloctenidae (scored 0). *Cebrenninus*: PME relictual, absent in some specimens (scored ?).

25. PME tapetum type: 0. Primitive. 1. Canoe. 2. Grate (fig. 12F). 3. Hexagonal pattern of holes uniformly distributed. Similarly as character 22. COMMENTS: *Hypochilus*: The primitive tapetum has bands of dark spots in the same disposition as the canoe lines of other Entelegynae. Homann (1971) reports that *Hypochilus* is unique in that the lenses are absent; the cuticle is only raised (scored 0). *Filistata*: from Homann (1951) (scored 0). *Eresus*: Eresidae without rods, no tapetum Homann (1971); the pigment in *Hersilia* (Hersiliidae) (Homann, 1951: fig. 24), has the same distribution as I saw in *Stegodyphus* (scored ?). *Oecobius*: PME modified tapetum, with a dark V-shaped line from the median side to the external side (scored ?). *Uloborus*: Secondary eyes without tapeta (Homann, 1971), as in Deinopidae (scored ?). *Araneus*: *Araneus redii* is different from *A. diadematus* (Homann, 1971), the PME-PLE with only external half of the canoe present, describing six loops, the half without tapetum has rhabdomes in rods, interpreted as a modified canoe tapetum by Homann and subsequent authors. In *Araneus diadematus* I see only a band of dark spots, as in the primitive type. Coded "canoe" after the interpretation of previous authors (scored 1). *Megadictyna*: observed by Diana Silva Dávila (personal commun.) (scored 1). *Nicodamus*: median line not well marked (fig. 12H) (scored 01). *Neoramia*: tapetum from Griswold et al. (2005) (scored 1). *Stiphidion*: from Gray and Smith (2004: 138): "Contrary to Homann (1971), followed by Griswold et al. (1999) and Gray and Smith (2002: 138), the eyes of *Stiphidion* (*S. facetum* ex Hornsby, NSW) lack grate-shaped tapeta; canoe-shaped tapeta are present in the ALE, but no tapeta are discernible in the posterior eyes." *Metaltella*: tapeta from cf. *Metaltella* sp. from Chile. *Calacadia*: from Homann (1971). *Cyrioctea*: canoe sinuous (scored 1). *Homalonychus*: the rhabdomes are curved (Homann, 1951, 1971) (scored 1). *Psechrus*: with parallel symmetry lines (scored 2). *Ctenus*: According to Homann (1971), in the Cteninae the rods are completely isolated. In this species, only the AME has isolated rods (scored 2). *Oxyopes*: Homann (1971) described the secondary eyes as diurnal, because they lack tapetum, noting that the structure is similar to that of lycosids, including the grate disposition of retinal rods. I scored all secondary eyes as grate (scored 2). *Cycloctenus*: no tapetum; according to Homann (1971), the eye morphology links *Cycloctenus* with Selenopidae (scored -). *Toxopsiella*: From Homann (1971: fig. 24). The rods are 3:1, not coffee-grain shaped, in rows, connected at the sides, similar as in *Tetragnatha*. There are remains of tapetum only on ALE (scored -). *Clubiona*: from Homann (1951). *Castianeira*, *Falconina*: I cannot see the median line (scored 01). *Agroeca*: see also Homann (1951). *Drassinella, Sesieutes*: all tapetum orientation deduced from general tapetum size, lines not visible (scored 01). *Hortipes*: visible in clove oil. *Anagraphis*: median lines not seen, only shape (scored 01). *Neoanagraphis*, Trachelidae ARG: I cannot see the line, only the geometry (scored 01). *Meedo*: reduced, displaced medially (scored ?). *Fissarena*: Canoe sinuous, displaced to the middle of the carapace. Platnick (2002) did not see the tapetum (scored 1). *Desognaphosa*: not very clear, but suggesting many holes in a median band (scored 01). *Ammoxenus*: see also Homann (1971). *Cheiracanthium*: tapeta from *C. inclusum* (scored 1). *Eilica*: only contour seen (scored 01). *Cheiramiona*: All tapeta scored "primitive" because instead of median lines, in all secondary eyes there are bands with some dark spots. The primitive tapetum in *Hypochilus* looks similar under the stereomicroscope (scored 0). *Eutichurus*: as in *Cheiramiona*, a median band with small dark spots (scored 0). Cf. Eutichuridae QLD: not good visibility (scored 01). *Zora*: in a key to families, Homann (1951) says that the posterior eyes of *Zora* lack tapetum (scored -). *Uliodon*: all tapeta with dark median irregular line (scored 1). *Griswoldia*: see also Griswold (1991: fig. 4). *Raecius*: from Griswold et al. (2005), see also Griswold (2002). *Zorocrates*: see also Homann (1971). *Philodromus, Tibellus*: from Homann (1975), all secondary eyes without tapetum (scored -). *Selenops*: Corronca (1997) cites a grate tapetum in posterior eyes of *Selenops*, but attributes these observations to Homann (1971), who reported a reduced tapetum with resemblances with those of Sparassidae and Cycloctemninae (scored ?). *Hovops*: I observed a lateral internal longitudinal line, but this can be just the border of a grate tapetum (scored ?). *Heteropoda*: Homann (1971, 1975) regarded the secondary eyes of heteropodids as unique, with many elements in common with those of philodromids (pigment distribution, rhabdome formation). He examined (1951, 1971) at least *Olios*, *Micrommata*, and *Heteropoda*, but did not comment on any Sparianthinae. The tapetum is very thin. The rhabdomes are not disposed in rods of two cells (scored 3). *Polybetes*: perforated in many places (scored 3). *Xysticus*: The retinal cells form rods of two cells, looking like coffee grains. These rods are isolated by the dark pigment, thus the loops of the tapetum are not seen. Secondary eyes of spiders with grate tapetum have high vitreus body, thus can form image (Homann, 1971; later he referred specifically to the thomisids) (scored 2). *Aphantochilus*: Subadult male examined, not good preparation but grate confirmed. Eyes examined by Homann (1975), described as in *Xysticus*. I have seen a grate tapetum with longitudinal symmetry in *Bucranium taurifrons* (scored 2). *Lyssomanes*: *Lyssomanes viridis* with retinal nuclei inside pigment cup (Homann, 1971), tapetum absent in all eyes (scored -). *Plexippus*: rhabdomes in rods (Homann, 1971), retinal nuclei outside the pigment cup (scored -).

26. PME tapeta symmetry axes: 0. Parallel to each other. 1. Orthogonal to each other (figs. 3A, 4J, 10B, F, L, 12A, C). Homann (1971) described this regular orientation of the tapeta as "gnaphosid" condition, but also reported the same orientation for *Phrurolithus*, at that time placed in Liocranidae. Dacke et al. (1999) found that the PME are efficient polarized light detectors and are used for navigation in *Drassodes cupreus*. Later, Dacke et al. (2001) found that several similarly shaped eyes in other gnaphosid genera do not polarize the light in the same way. COMMENTS: *Liocranum*: line not seen but symmetry evident (scored 1). *Xenoplectus*: perhaps a bit less than 90°, also displaced to the internal side of the cup (scored 1). *Pseudolampona*: about 1/2 diameter (scored 0). *Micaria*: from Homann (1971) (scored 1). *Eilica*: slightly more than 90° (scored 1). *Austrachelas*: specimen clarified in clove oil, tapetum not well preserved, only right PME contour was sufficiently distinctive for orientation (scored 1). *Meedo*: thin, internal, not 90°, even a little open posteriorly (scored 0). *Macerio*: symmetry inferred from curvature only (scored 0). *Polybetes*: a median darker line may suggest a longitudinal axis (scored -). *Stephanopoides*: slightly opening posteriorly, about 30° each eye (scored 0).

27. PME tapetum width: 0. At least about 1/2 diameter of eye or more. 1. Narrow, less than 1/2 diameter of eye. A character used for Araneoidea (e.g., Griswold et al., 1998; Scharff and Coddington, 1997). COMMENTS: *Mimetus*: very wide (scored 0). *Legendrena*: undefined, as the eyes themselves are narrow (scored 01). *Pseudolampona*: about 1/2 diameter (scored 0). *Zorocrates*: See also Homann (1971: fig. 27B). Both PME and ALE with a sinuous dark line (scored 1).

28. PLE and PME tapeta axes orthogonal, coplanar: 0. Absent. The PLE tapetum is not coplanar and orthogonal with PME tapetum (several orientations found). 1. Present.

Prodidomines have a peculiarly procurved posterior eye row with flat lenses. At least in *Prodidomus* the PLE and PME tapeta are orthogonal to each other, suggesting that the PLE are also part of the polarized light detector system, together with the PME. The examined specimens of *Neozimiris* had the tapeta damaged, but the eye lens disposition is the same (Ubick, 2005: fig. 51.6), a pattern that occurs in *Zimiris* as well (Platnick and Penney, 2004: fig. 1), and seems to be a synapomorphy for Prodidominae, perhaps together with Molycriinae (see Platnick and Baehr, 2006: figs. 4–10).

29. Clypeus margin profile: 0. Straight or slightly curved (fig. 4I). 1. Produced in a median lobe (fig. 11F). The clypeus is prolonged in the midline, between the chelicerae. Proposed as a synapomorphy of Austrochiloidea (Forster et al., 1987), appears also scattered in Eresidae (Griswold et al., 2005), *Sesieutes*, *Oedignatha* (fig. 14B), and some trochanteriids (fig. 11C, D). COMMENTS: *Psechrus*: prolonged at midline but becoming gradually membranous (scored 01).

30. Chilum: 0. Present (figs. 3A 13D, 14C). 1. Absent (fig. 14G). COMMENTS: *Stiphidion*: very slightly sclerotized cuticle (scored 0). *Cryptothele*: a narrow, wide, pilose band (scored 0). *Psechrus*, *Acanthoctenus*, *Vulsor*, *Ctenus*, *Oxyopes*, *Dolomedes*, *Toxopsiella*, *Odo bruchi*: clypeus becoming gradually membranous, continuing flat with membrane bearing the chilum (scored 0). *Senoculus*: area below clypeus soft, deeply recessed together with chelicerae (scored 1). *Oedignatha*: coded as clypeus produced into median lobe (char. 29), probably a fused chilum, as it grows beyond the carapace reborder (fig. 14B) (cf. Platnick, 2000: char. 12) (scored 1). Cf. Gnaphosoidea TEX: chelicerae arising from deep inside the carapace, area not exposed (scored ?). *Neato*: only a slightly sclerotized surface without defined borders (scored 1). *Camillina*: small, recessed (scored 0). *Doliomalus*: recessed (scored 0). *Platyoides*: a median hump, not well sclerotized (scored 01). *Zora*: weakly sclerotized (scored 0). *Epidius*: faint, very pale (scored 0). *Tmarus*: faint median sclerotization (scored 01).

31. Chilum configuration: 0. Single median sclerite (figs. 3A, 13D, F, 14C). 1. Paired isolated sclerites (fig. 14A). COMMENTS: *Eriauchenius*: plates distant from each other (scored 1). *Psechrus*: very weakly sclerotized (scored 1). *Corinna*: bilobed (fig. 14C) (scored 0). *Trachelas mexicanus*: bulging halves, slightly sclerotized on median suture (scored 1). *Paccius*: with a projecting horn (scored 0). *Mandaneta*: median, bilobed, protruding (scored 0). Cf. Eutichuridae QLD: with small median protuberance (scored 0). *Macerio*, *Strotarchus*, *Cebrenninus*: median, bilobed (scored 0). *Hovops*: weakly sclerotized, weaker in the middle (scored 01).

32. Chelicerae-labrum distance: 0. Narrow. The space between chelicerae and mouthparts is narrow, membranous (fig. 12D). 1. Wide diastema. There is an ample space between the chelicerae and the mouthparts (Schütt, 2002) (figs. 7E, 11E).

33. Sclerotization between chelicerae and labrum: 0. Membranous (figs. 7E, 12D). 1. Sclerotized, continuous with carapace margins (fig. 11E). COMMENTS: *Storenomorpha*: narrow diastema with a sclerotized band, not fused to carapace sides (scored 0).

CHELICERAE

The chelicera has a thick basal article, the paturon, and a pointed articulated fang with the venom outlet near the tip (fig. 15A, C). The venom gland is covered by muscles in a characteristic helix pattern (fig. 15A). The paturon may have a large convex boss (fig. 15D) opposing a corresponding concavity in the anterior margin of the carapace. The ectal side of the paturon may have a file of stridulatory ridges (fig. 15E). The paturons articulate against each other on a median line, at which posterior end there is a single, small intercheliceral sclerite (fig. 16A); on the paturon, near the intercheliceral sclerite, there may be a basal posterior membranous mound (fig. 16C) nearby. The mesal margin of the paturon may be prolonged in cheliceral lamina (fig. 15F), acting as a chela opposing the fang. When folded, the fang rests on a furrow (fig. 15C). The cheliceral gland opens through a field of rimmed pores, approximately opposing the venom outlet. The anterior and posterior margins of the furrow (promargin and retromargin) are usually adorned with series of teeth and specialized setae (fig. 15B). Immediately anterior to the

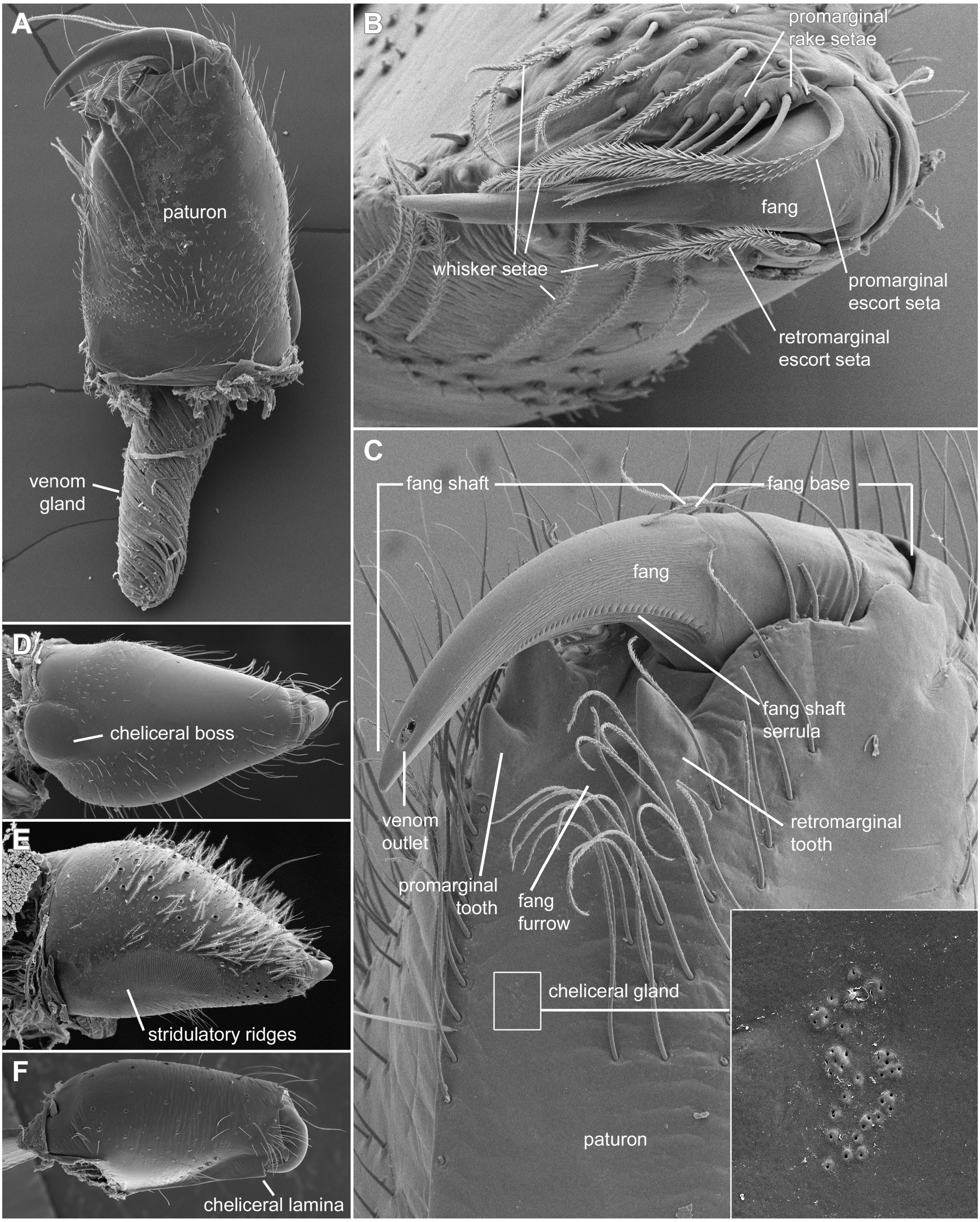

A
paturon
venom gland
B
promarginal rake setae
fang
whisker setae
promarginal escort seta
retromarginal escort seta
C
fang shaft
fang base
fang
fang shaft serrula
venom outlet
promarginal tooth
fang furrow
retromarginal tooth
cheliceral gland
paturon
D
cheliceral boss
E
stridulatory ridges
F
cheliceral lamina

Fig. 15. Structures of chelicerae, female. **A.** *Gayenna americana* (Anyphaenidae). **B.** *Phrurotimpus alarius* (Phrurolithidae) apical. **C.** *Plexippus paykulli* (Salticidae). **D.** *Xiruana gracilipes* (Anyphaenidae). **E.** *Sicarius rupestris* (Sicariidae). **F.** *Drymusa rengan* (Drymusidae).

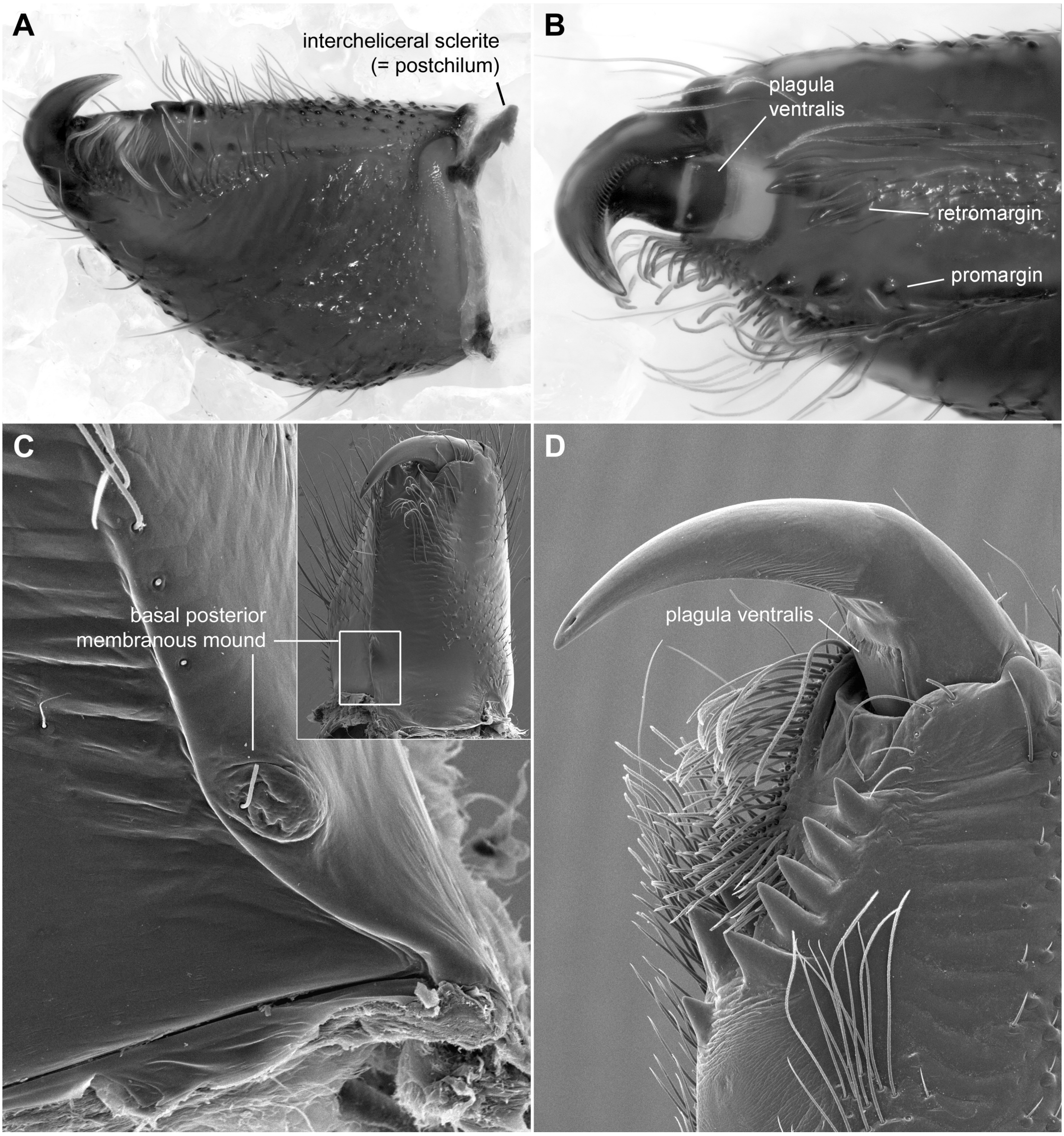

A
interchelicral sclerite
(= postchilum)
B
plagula
ventralis
retromargin
promargin
C
basal posterior
membranous mound
D
plagula ventralis

Fig. 16. Structures of chelicerae, female. **A.** *Trachelas mexicanus* (Trachelidae), mesal. **B.** Same, mesal-posterior. **C.** *Plexippus paykulli* (Salticidae; image by Junxia Zhang). **D.** *Falconina gracilis* (Corinnidae).

fang base there is a rake or shield made of a line of bowed setae with aligned barbs, the *promarginal rake setae*. There may be second, more proximal line or group modified, fluffy setae, the *whisker setae*. The more ectal of the whisker setae is usually modified as a *promarginal escort seta*, much longer, bent near its base and accompanying the fang. There may be a similar group of whisker setae on the retromargin, including a *retromarginal escort seta*. The fang articulates on two strong condyles. In the mesal articular membrane between the fang and the paturon there is a small sclerite, the plagula ventralis (fig. 16B), where the fang flexor tendon attaches. The fang has two sections, a short, smooth base, and a longer shaft, usually with longitudinal striae and a posterior internal serrula (fig. 15C).

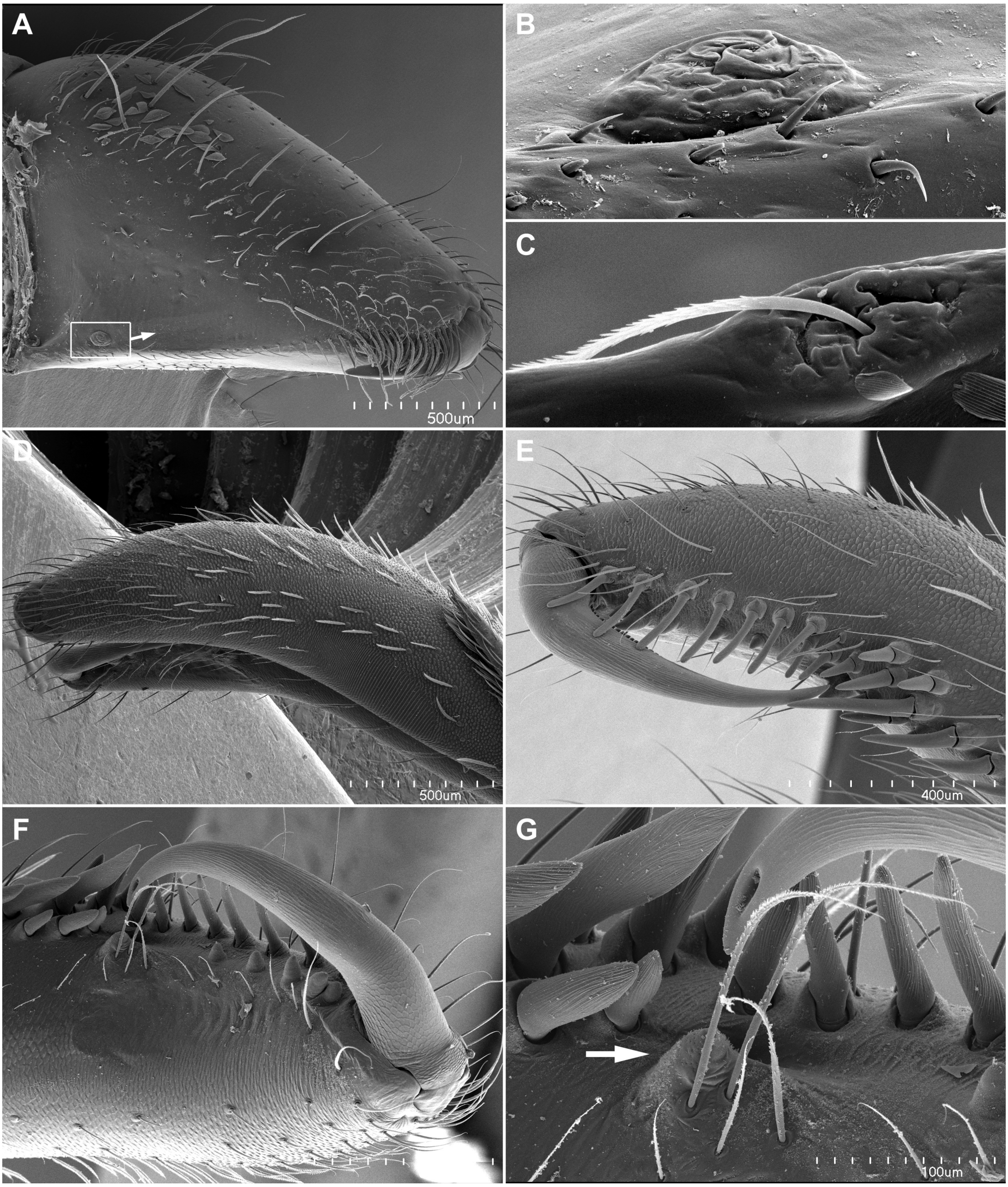


Fig. 17. Structures of chelicerae, female. **A.** *Oxyopes heterophthalmus* (Oxyopidae). **B.** Same, detail of basal posterior membranous mound, inset marked on A. **C.** *Evarcha falcata* (Salticidae; image by Junxia Zhang), basal posterior membranous mound. **D.** *Eriauchenius workmani* (Archaeidae), stridulatory file. **E.** Same, fang and peg teeth. **F.** Same, fang and cheliceral mound. **G.** Same, close-up, arrow to cheliceral mound.

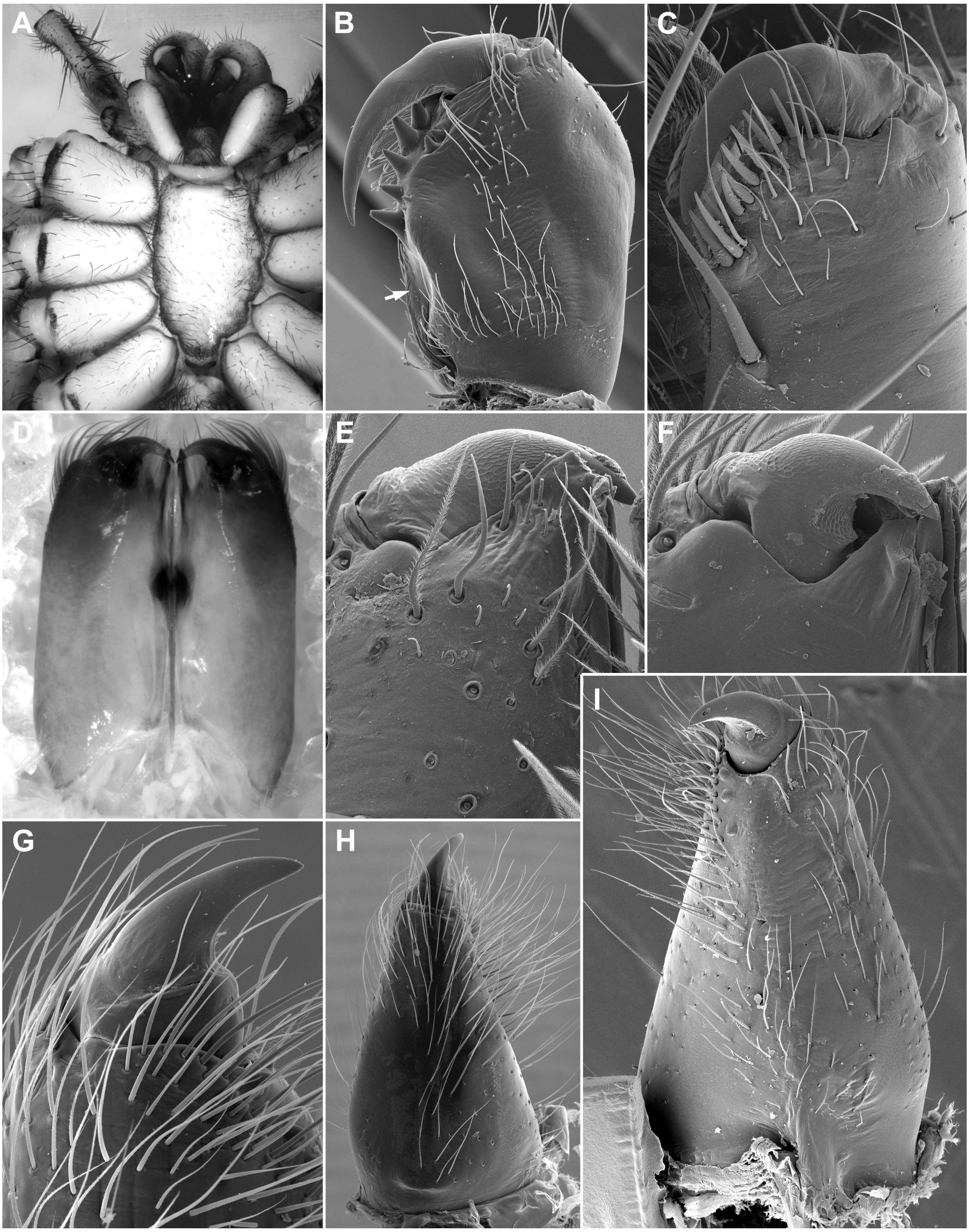


Fig. 18. Chelicerae of female. **A.** *Hypochilus pococki* (Hypochilidae), cephalothorax and chelicerae. **B.** *Hypochilus pococki* (Hypochilidae), left, posterior view, arrow to median cheliceral concavity. **C.** *Mimetus hesperus* (Mimetidae), right, anterior view of promargin. **D.** *Kukulcania hibernalis* (Filistatidae) posterior view. **E.** *Filistata insidiatrix* (Filistatidae), left, anterior view of promargin. **F.** Same, posterior view of right fang and cheliceral lamina. **G.** *Ariadna boesenbergi* (Segestriidae) female, left chelicera, anterior view of promargin. **H.** Same, chelicerae ectal view. **I.** Same, posterior-mesal view.

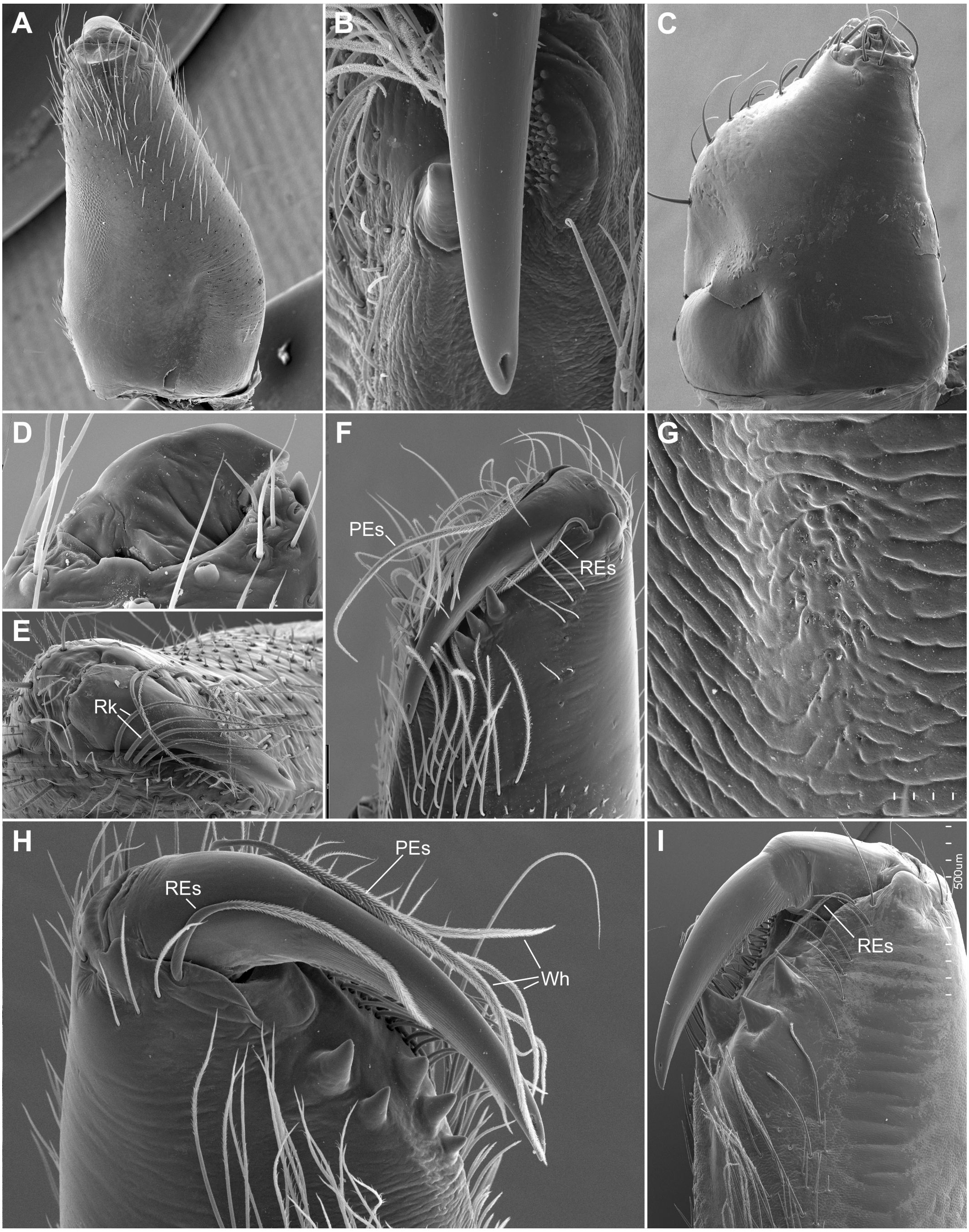


Fig. 19. Chelicerae, female (all left, except C, right). **A.** *Thaida peculiaris* (Austrochilidae) ectal view. **B.** Same, venom outlet and teeth. **C.** *Uloborus glomosus* (Uloboridae) ectal view. **D.** *Zodarion italicum* (Zodariidae) fang and promargin, anterior view. **E.** *Homalonychus theologus* (Homalonychidae) fang and promargin anterior-distal view. **F.** *Ciniflella* ARG (Tengellidae) posterior view. **G.** *Donuea* sp. ("Liocranidae") cheliceral gland. **H.** *Paravulsor* sp. (Miturgidae) posterior view. **I.** *Clubiona pallidula* (Clubionidae) posterior view.

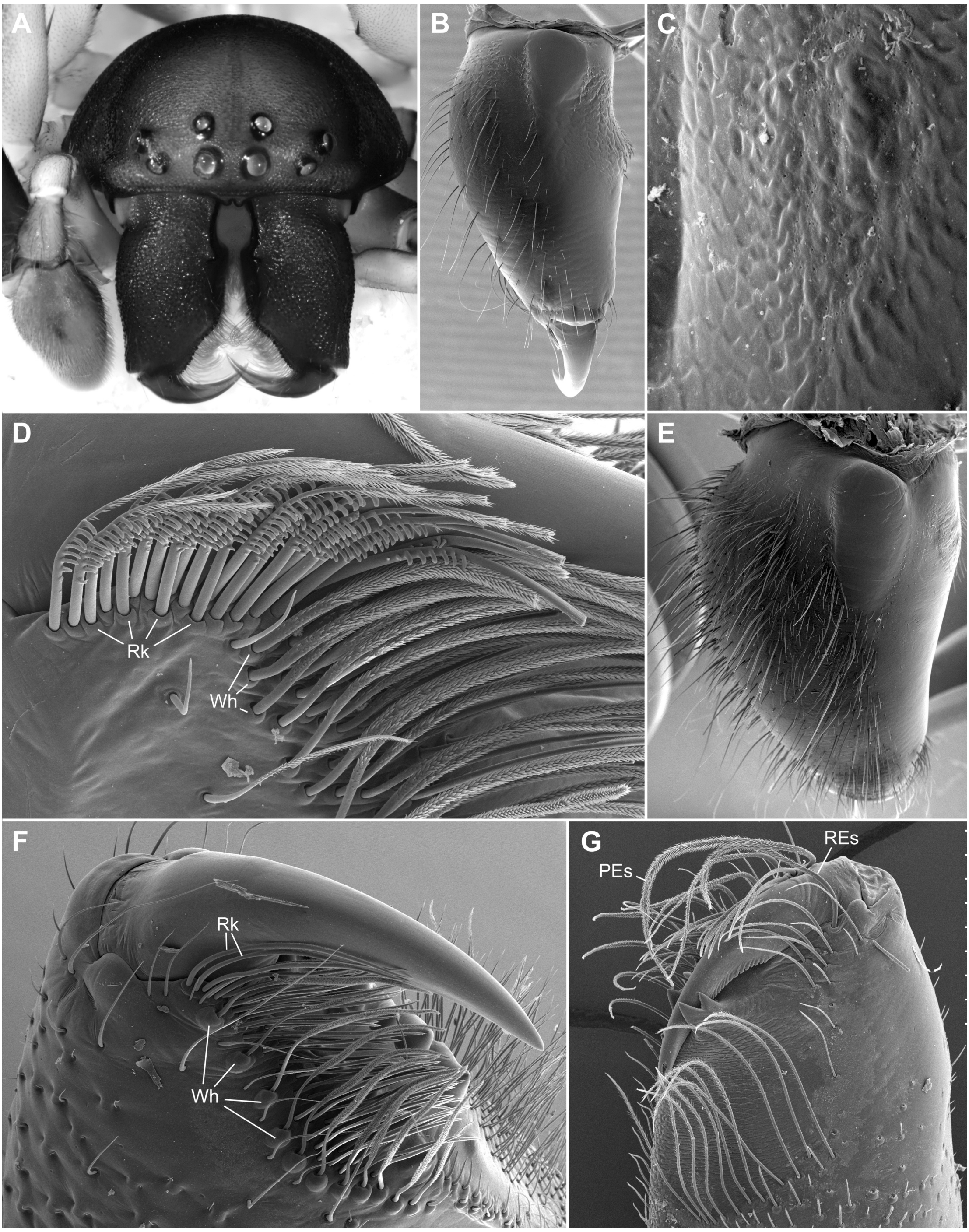


Fig. 20. Chelicerae. **A.** *Mandaneta sudana* (Corinnidae) male with modified chelicerae. **B.** Cf. *Medmassa* THA (Corinnidae) subadult female. **C.** Same, cheliceral gland. **D.** *Copa flavoplumosa* (Corinnidae) female. **E.** *Polybetes pythagoricus* (Sparassidae) female. **F.** *Paccius* cf. *scharffi* (Trachelidae), female. **G.** *Otacilia* sp. (Phrurolithidae) female.

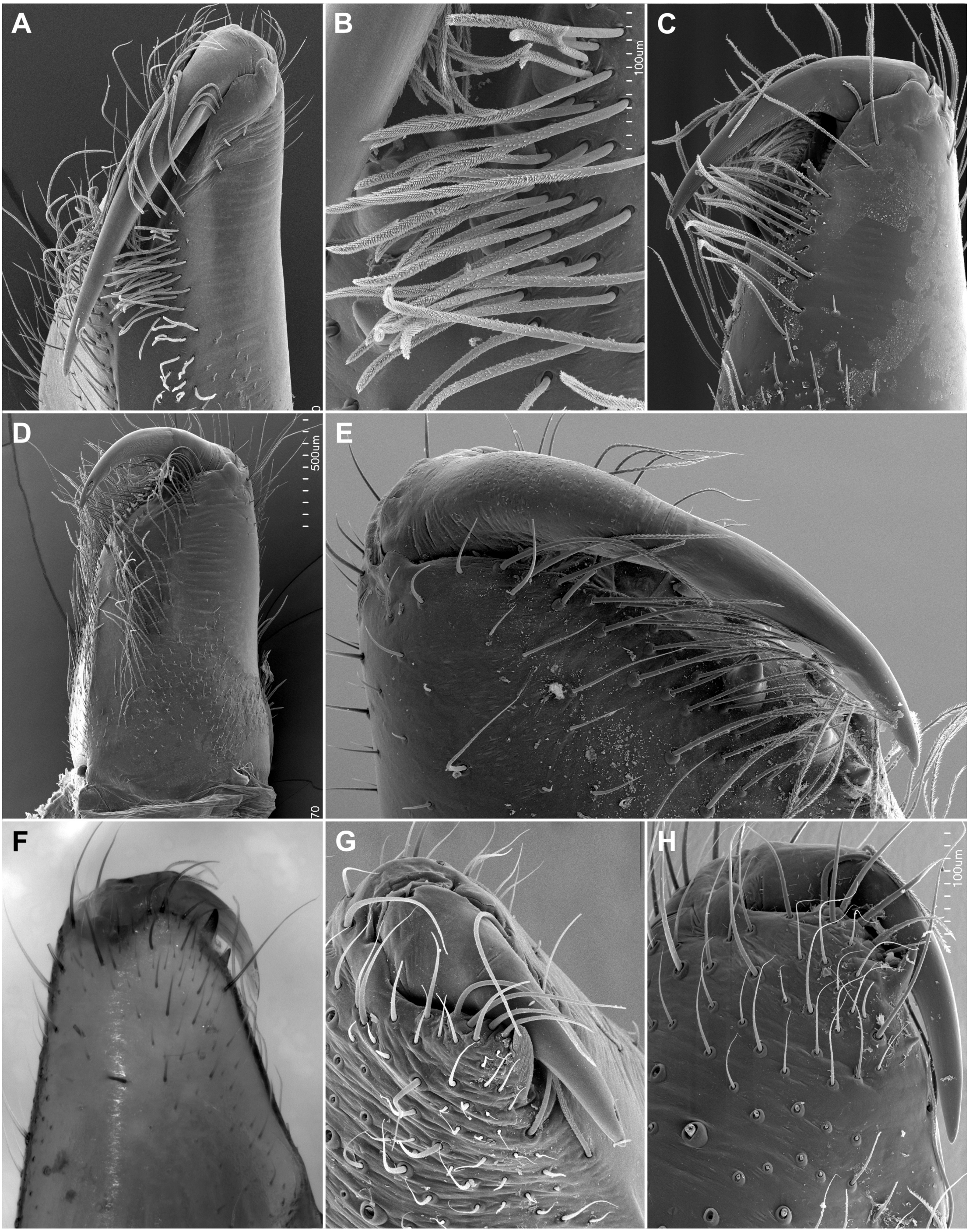


Fig. 21. Chelicerae of female. **A.** *Cheiramiona* sp. Uzungwa (Eutichuridae). **B.** Same, detail of group of whisker setae. **C.** Eutichuridae MAD (Eutichuridae). **D.** *Holcolaetis* cf. *zuluensis* (Salticidae). **E.** *Lyssomanes viridis* (Salticidae). **F.** *Tibellus oblongus* (Philodromidae). **G.** *Petrichus* sp. (Philodromidae). **H.** *Philodromus aureolus* (Philodromidae).

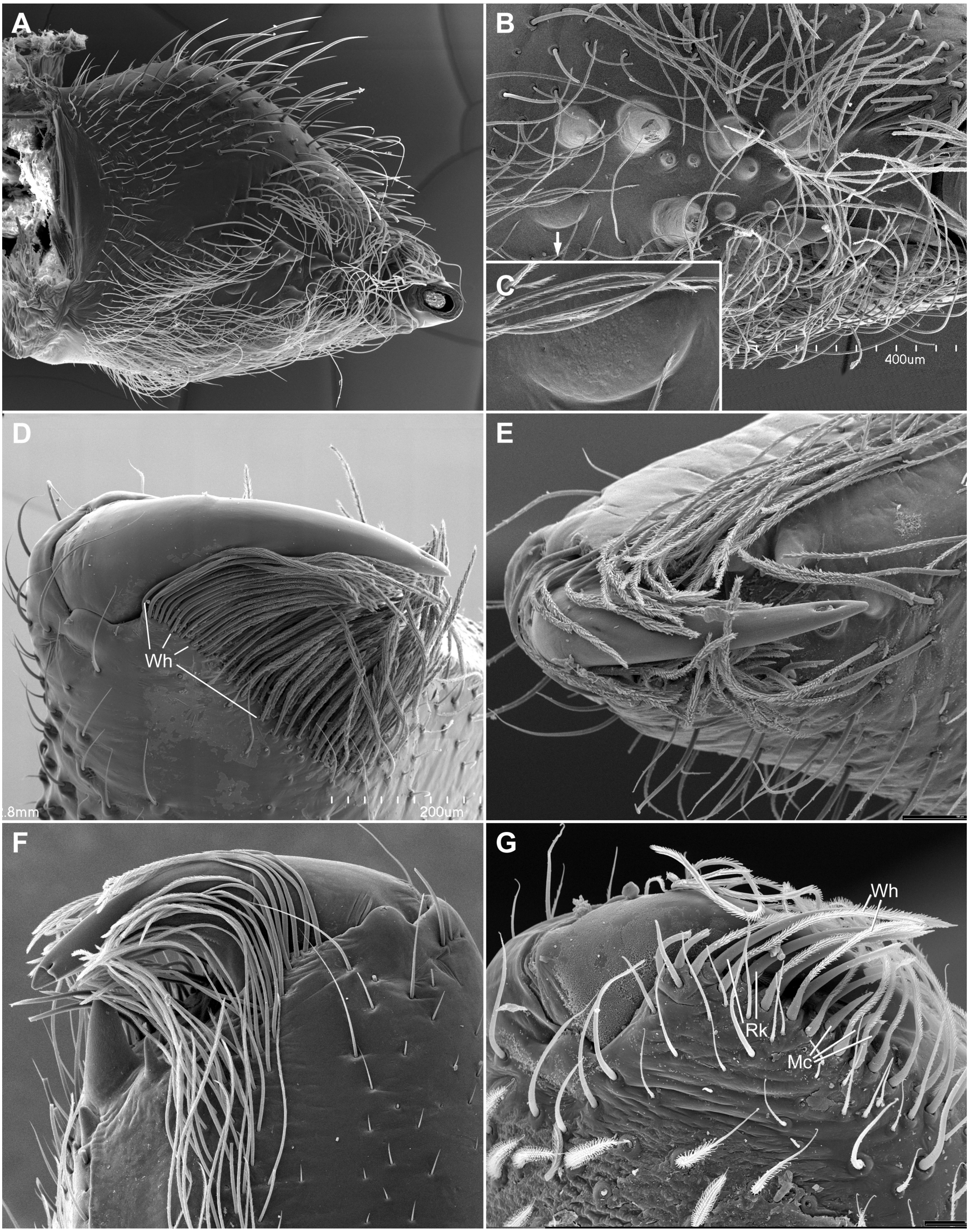


Fig. 22. Chelicerae of Thomisidae, female (except G, subadult female). **A.** *Borboropactus bituberculatus*. **B.** Same, cheliceral teeth. **C.** Same, cheliceral gland. **D.** *Cebrenninus rugosus*. **E.** *Stephanopis ditissima*. **F.** *Stephanopoides sexmaculata*. **G.** *Boliscus* cf. *tuberculatus*.

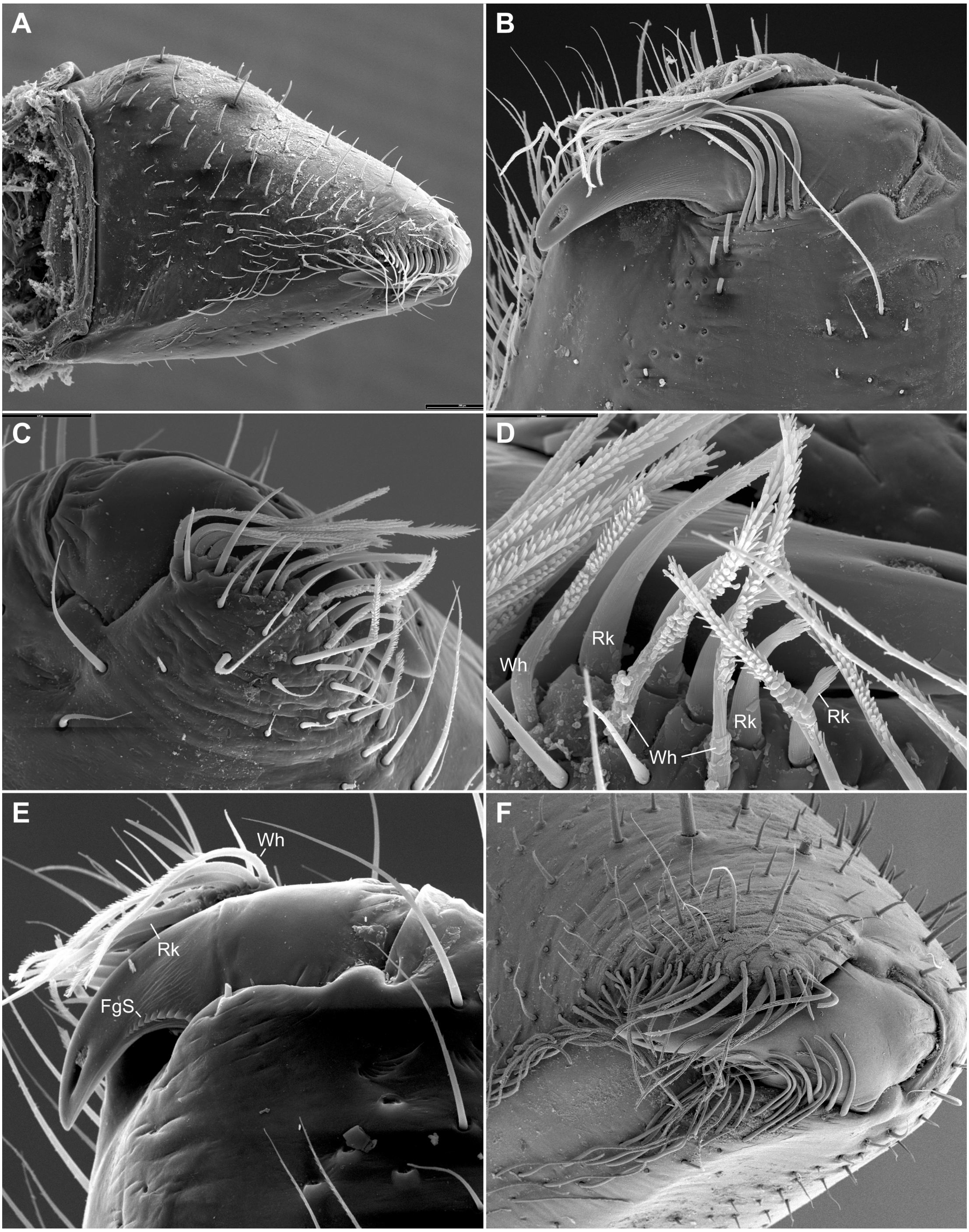

A
B
C
D
Rk
Wh
Rk
Rk
Wh
E
Wh
Rk
FgS
F

Fig. 23. Chelicerae of Thomisidae, female. **A.** *Thomisus onustus*. **B.** Same, fang and retromargin. **C.** *Tmarus holmbergi*. **D.** Same, detail. **E.** Same, fang and retromargin. **F.** *Xysticus cristatus*.

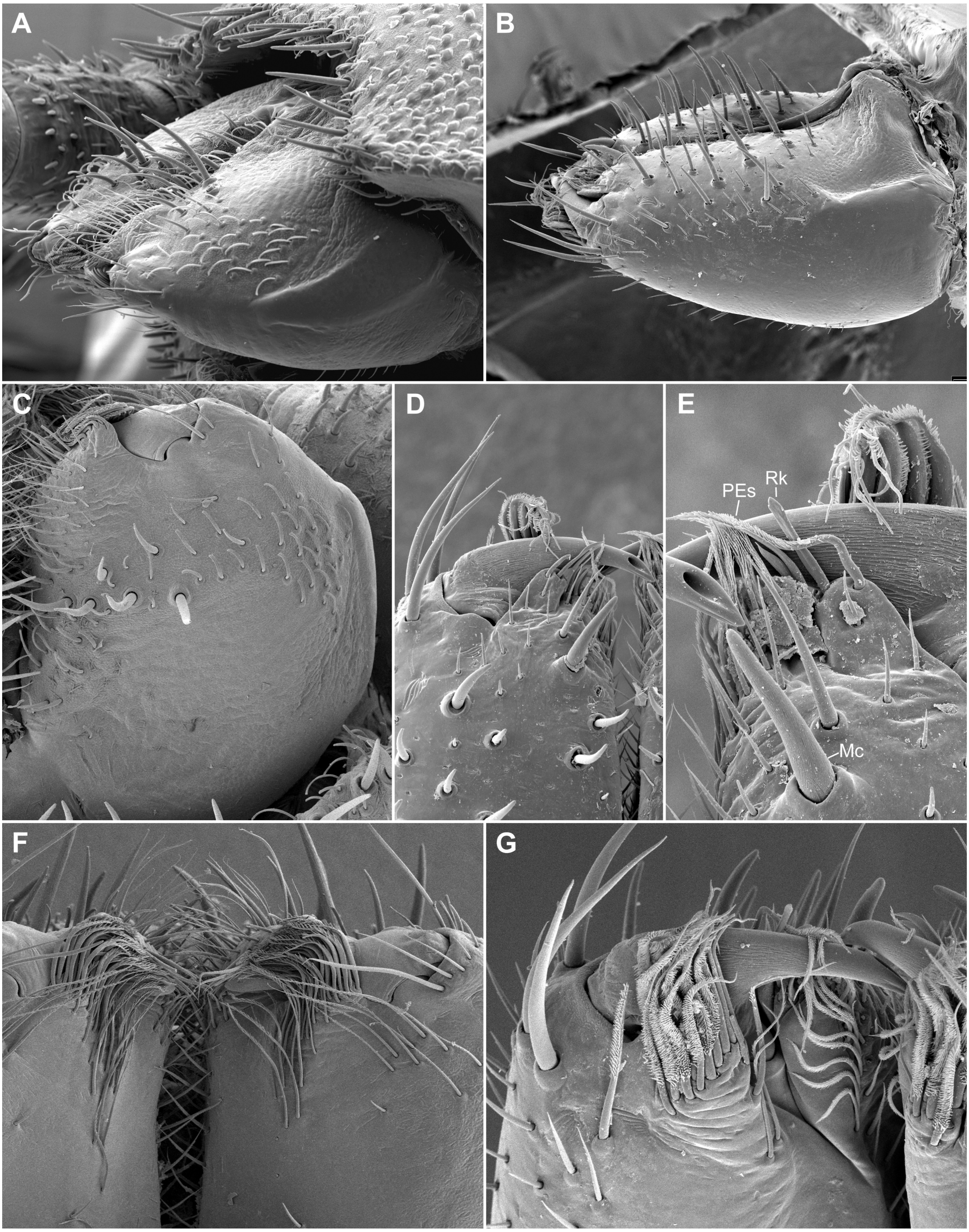


Fig. 24. Chelicerae of Aphantochilinae and Strophiinae (Thomisidae), female. **A.** *Aphantochilus rogersi*, lateral view. **B.** *Strophius albofasciatus*, lateral view. **C.** *Aphantochilus rogersi*, anterior view. **D.** *Strophius albofasciatus*, anterior view. **E.** Same, detail. **F.** *Aphantochilus rogersi*, posterior view. **G.** *Strophius albofasciatus*, posterior view.

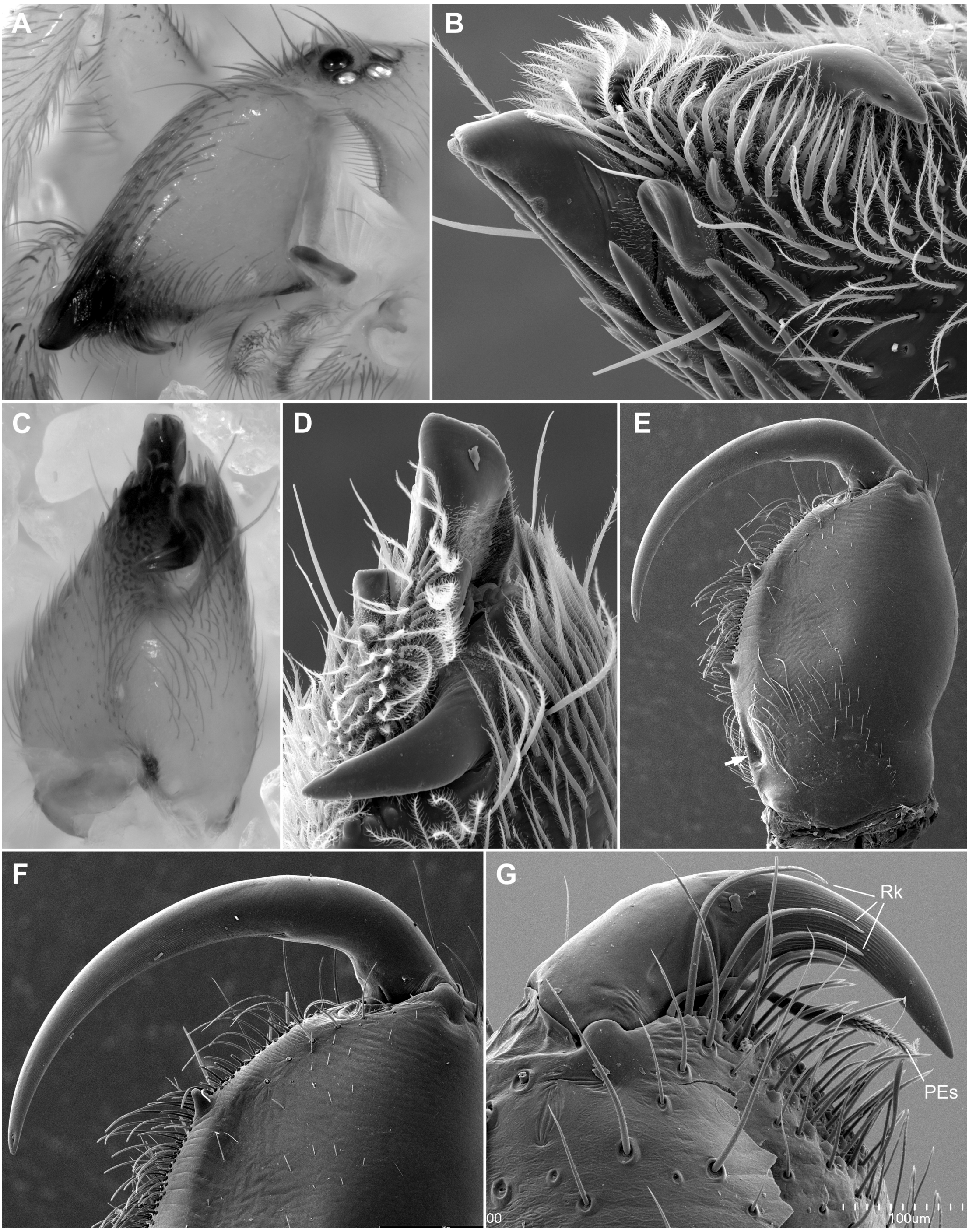


Fig. 25. Chelicerae of female. **A.** *Rastellus florisbad* (Ammoxenidae) female. **B.** Same, left chelicera mesal. **C.** Same, detail of promargin. **D.** Same, retromargin. **E.** *Platyoides walteri* (Trochanteriidae) female. **F.** Same, detail. **G.** *Cithaeron delimbatus* (Cithaeronidae) female.

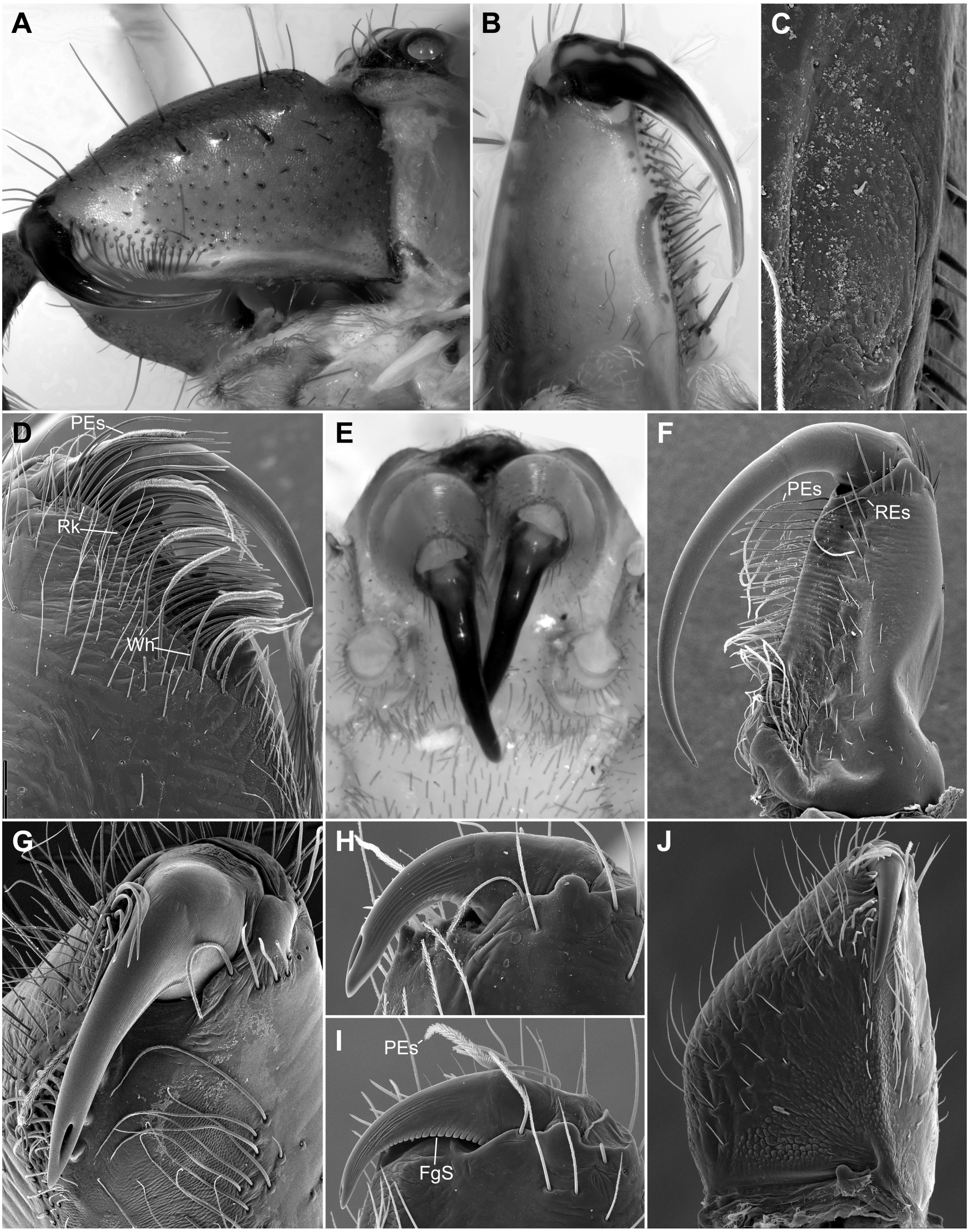


Fig. 26. Chelicerae of female. **A.** *Galianoella leucostigma* (Gallieniellidae). **B.** Same, posterior view. **C.** Same, cheliceral gland and membranous area. **D.** *Austrachelas pondoensis* (Gallieniellidae). **E.** *Meedo houstoni* (Gallieniellidae), arrow to median cheliceral concavity. **F.** Same, posterior view. **G.** *Lampona cylindrata* (Lamponidae). **H.** *Pseudolampona emmett* (Lamponidae). **I.** *Lamponella brookfield* (Lamponidae). **J.** Same, mesal view.

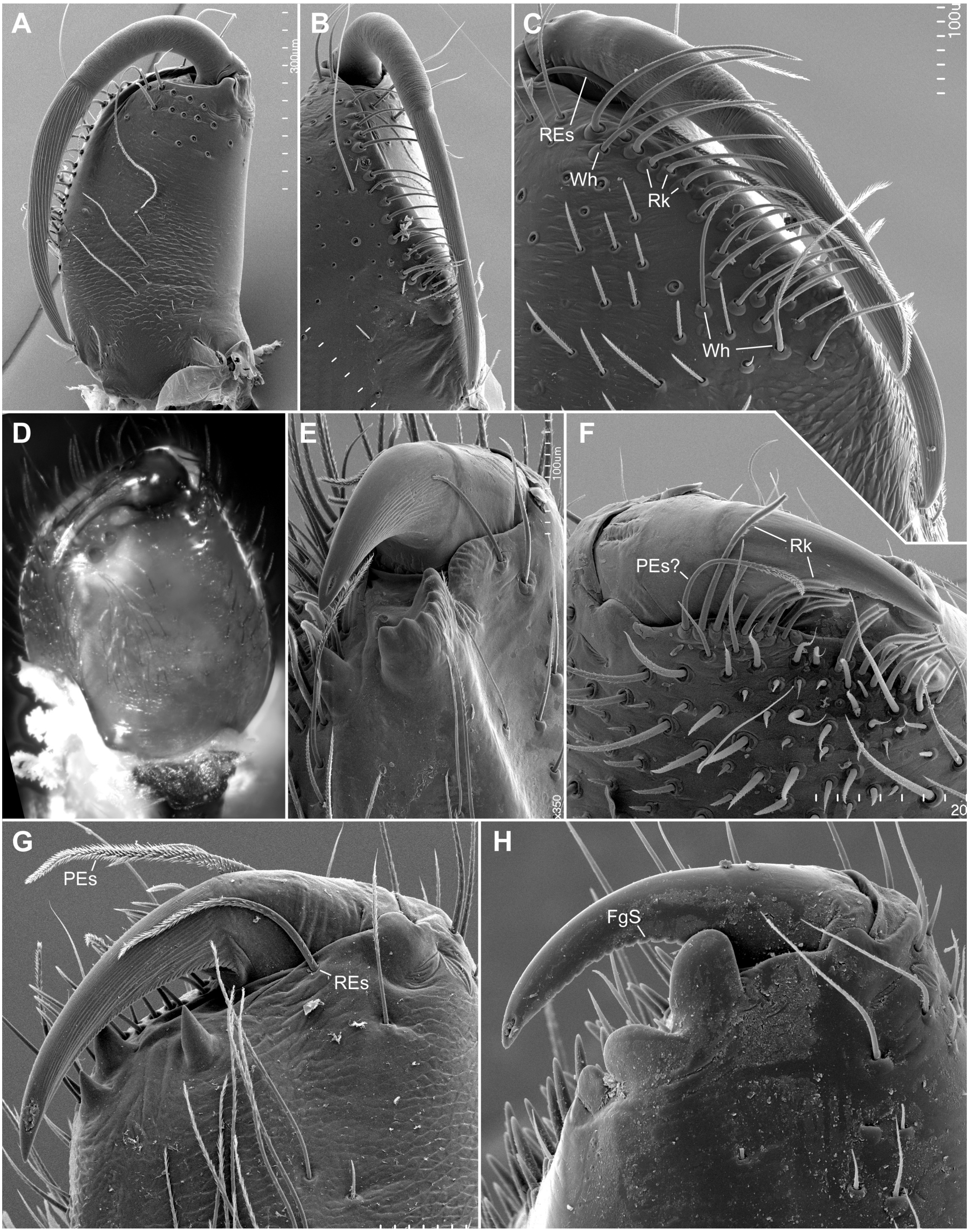

A
300um
B
C
100u
REs
Wh
Rk
Wh
D
E
100um
x350
F
Rk
PEs?
20
G
PEs
REs
H
FgS

Fig. 27. Chelicerae of female. **A.** *Prodidomus redikorzevi* (Prodidomidae), posterior view. **B.** Same, mesal view. **C.** Same, anterior view. **D.** *Vectius niger* (Gnaphosidae). **E.** *Gnaphosa sericata* (Gnaphosidae), mesal view. **F.** Same, anterior view. **G.** *Micaria fulgens* (Gnaphosidae). **H.** *Eilica* sp. (Gnaphosidae).

34. Gallieniellid cheliceral shape (tubuliform, porrect): 0. Absent, fangs diaxial, paturon not tubuliform. 1. Present, fangs paraxial, paturon tubuliform (figs. 13D, 26E). COMMENTS: *Hypochilus*: intermediate between paraxial and diaxial according to Kraus (1975), but not tubuliform (fig. 18A) (scored 0). *Oecobius*: there is a long anterior shaft inserting into carapace (scored 0).

35. Cheliceral basal posterior membranous mound: 0. Absent (fig. 21D). 1. Present (figs. 16C, 17A–C). The posterior membranous mound was described by Maddison (1988, 1996: 226) as "a mound of slit sense organs with an associated seta on the medial edge of the chelicera," and proposed as a synapomorphy of the salticoid division of Salticidae. Upon examination under SEM, it is not clear that the depressions correspond to slit sensilla, which otherwise occur in relatively hard cuticle (Barth, 2002; those of the ALS are on softer cuticle, but have a different appearance). COMMENTS: *Cyrioctea*: large (scored 1). *Oxyopes*: well defined, but dark (fig. 17A, B) (scored 1). *Meriola*: also oblique median ridge as in *Trachelas minor* (scored 0). *Trachelopachys*: distinct, but sclerotized (scored 0). *Neozimiris*: low sclerotized mound (scored 0). *Meedo*: large fleshy lobe, all area unsclerotized, but distal to the cheliceral gland, which is scored separately (scored 0). *Doliomalus*: not in the same place as in Salticidae, a whitish spot (scored 0). *Syspira*: sclerotized ridge (scored 0). *Strotarchus*: there is a paler area (scored 0). Eutichuridae MAD: looks sclerotized in the stereomicroscope (scored 1). *Philodromus*: more advanced, larger than in salticids (scored 1). *Petrichus*: at the end of a whitish ridge (scored 1). *Polybetes*: just a slightly less sclerotized area (scored 0). *Eusparassus*: not well defined, bearing some setae (scored 01). *Titanebo*: there is an unsclerotized notch, but more posterior than in salticids or oxyopids (scored 0). *Tmarus*: only a whitish area (scored 0). *Strophius*: large, with some setae (scored 1).

36. Extension of anterior part of cheliceral insertion: 0. Not protruding anteriorly (figs. 23A, 24A). 1. Protruding anteriorly on median line (fig. 24B). Seemingly related with the ability to extend the chelicerae up and forward while holding an ant (see char. 392). COMMENTS: *Eriauchenius*: all borders protruding (scored 01). *Ammoxenus*: the anterior face of the chelicerae is protruding, but the insertion is normal (scored 0). *Tmarus*: not protruding, but the chelicera can be considerably bent upward (scored 0).

37. Cheliceral stridulatory ridges: 0. Absent, ectal side of paturon smooth (fig. 20B). 1. Present, file of ridges on the ectal side of the paturon (figs. 17D, 19A). COMMENTS: *Thaida*: females with aligned nodules with pores (Forster et al., 1987) (fig. 19A) (scored 1).

38. Cheliceral boss: 0. Absent (figs. 7E, 19A). 1. Present (figs. 19C, 20E, B). Note that this is not related to spider size, i.e., the boss is absent in some big spiders, e.g., *Hypochilus*, *Thaida*. COMMENTS: *Uloborus*: not large but evident (fig. 19C) (scored 1). *Platyoides*: a large patch with different texture may mark the area homologous with the boss (scored 0).

39. Cheliceral boss size: 0. Small (fig. 19C). 1. Large (fig. 20B). In this dataset there is no clearcut distinction in terminals having a particularly small cheliceral boss, except for *Uloborus* (fig. 19C). COMMENTS: *Araneus*: supposedly small in Orbicularians (Griswold et al., 2005), I do not see a clear-cut difference (scored 1). *Oxyopes*: very elongate. *Phrurotimpus, Otacilia*: shallow (scored 1). *Teutamus*: shallow but large (scored 1). *Meedo, Neato*: very large, whitish (scored 1). *Aphantochilus*: very long, reaching half of paturon (fig. 24A) (scored 1). *Holcolaetis, Portia*: narrow, between two notches (scored 1). *Hispo*: Between two notches (scored 1).

40. Cheliceral lateral basal transverse ridge: 0. Absent, surface smooth or convex. 1. Present, a short transverse ridge on an elevated area, opposed to the anterior lateral corner of the carapace. Present only in *Ariadna* (fig. 18H).

41. Male chelicerae medial surfaces: 0. About parallel. 1. Excavated (fig. 20A). This condition also occurs in a group of species of the genus *Philisca* (Ramírez, 2003). COMMENTS: *Mandaneta*: also an anterior median pointed projection (scored 1). Trachelidae ARG: slightly so (scored 01). *Eilica*: male and female (scored 01). *Austrachelas*: male chelicerae very rugose anteriorly (scored 0).

42. Median cheliceral concavity: 0. Absent. 1. Present (figs. 18B, 25E), a depression on the paturon fitting the tip of the fang (see Griswold et al., 2005: char. 37). COMMENTS: *Cryptothele*: a small, well-delimited depression, but not on fang tip (scored 0). *Neozimiris*: very small depression (scored 01). *Copa*, *Galianoella*, *Lauricius*: shallow depression (scored 01).

43. Cheliceral gland mound: 0. Absent, gland on a flat or depressed patch (figs. 19G, 20C, 26C). 1. Present, gland on a mound (fig. 17G). COMMENTS: *Filistata*: gland not found with SEM (scored ?). *Huttonia*: from Forster and Platnick (1984) (scored 1). *Pronophaea*, *Teutamus*: cheliceral gland not seen in SEM (scored ?). *Galianoella*: gland on membranous patch (fig. 26C) (scored 0). *Meedo*: the area looks raised because there is a more anterior flexible area (scored 0). *Amaurobioides*, *Macerio*: observed with stereomicroscope (scored 0). *Borboropactus*: shallow but well-defined mound (fig. 22B, C) (scored 01). *Cocalodes*: a very low mound (scored 01).

44. Cheliceral retromargin and furrow sclerotization: 0. Retromargin and furrow sclerotized (fig. 16B). 1. Unsclerotized posterior patch just distal from cheliceral gland area (fig. 27D). 2. All cheliceral retromargin and furrow unsclerotized (fig. 26A, B). States are ordered. COMMENTS: *Mimetus*: much of the short furrow is unsclerotized (scored 1). *Calacadia*: elongate white patch (scored 1). *Cybaeodamus*: unsclerotized band reaching the basal unsclerotized mound (scored 2). *Hortipes*: too pale to see (scored ?). *Galianoella*: the unsclerotized area surrounds the teeth, and unites with the anterior unsclerotized patch (scored 2). *Meedo*: all internal side white (scored 2). *Neato*: the chelicera is basically the same as in the SEMs of *Meedo*, the membranous area less evident (scored 2). *Ammoxenus*: entire posterior face unsclerotized (scored 2). *Rastellus*: large unsclerotized area anterior-distal to the teeth (fig. 25B) (scored 01). *Eilica*: basal tooth arising from membranous area (scored 1). *Neozimiris*: all pale (scored ?). *Eusparassus*: mesal margin weakly sclerotized, from base to teeth, with darker cheliceral gland patch (scored 0). *Stephanopoides*: base of large tooth and part of promargin unsclerotized (scored 12).

45. Cheliceral fleshy lobes: 0. Absent. 1. Present. In this dataset only *Filistata* has two fleshy lobes anterior and posterior to the cheliceral chela (fig. 18E, F).

46. Cheliceral lamina: 0. Absent (fig. 18I). 1. Present, the mesal margin of the cheliceral paturon projecting in a chela (figs. 15F, 18F). COMMENTS: *Stegodyphus*: distal protuberance, not continuous from base (scored 01). *Neoramia*: mesal ridge prolonged in a small chela with basal tooth (scored 01). *Storenomorpha*: mostly membranous (scored 1).

47. Cheliceral promarginal teeth: 0. Present, at least one (fig. 15C). 1. Absent (figs. 17E, 27B). An experimental character scoring the teeth number as ordered states (0, 1, 2, 3, 4, 5, 6–8) was highly incongruent with the phylogenetic tree. COMMENTS: *Filistata*: one large tooth between the two fleshy lobes is the chela or lamina, may be pro- or retromarginal, not considered homologous to a tooth (scored 1). *Eresus*: a group of five teeth on a mound, perhaps three promarginals and two retromarginals (scored ?). *Stegodyphus*: a group of six teeth in two rows, on a mound, probably four promarginals and two retromarginals (scored ?). *Nicodamus*: Harvey (1995: fig. 8) interpreted as one promarginal tooth (scored 0). *Cycloctenus*: teeth in a basal line! (scored 0). *Toxopsiella*: from Forster and Blest (1979) (scored 0). *Homalonychus*: small (scored 0). Cf. Gnaphosoidea TEX: very small teeth, seen in male digested with KOH (scored 0). *Eilica*: two small anterior teeth interpreted as promarginals (scored 0).

48. Cheliceral retromarginal teeth: 0. Present, at least one (figs. 15C, 27G). 1. Absent (fig. 26G). An experimental character scoring the teeth number as ordered states (0, 1, 2, 3, 4, 5, 6 or more) was highly incongruent with the phylogenetic tree. COMMENTS: *Eriauchenius*: five plus the mound (scored 0). *Gnaphosa*: serrate chela (scored 1). *Eilica*: three flat, rounded processes interpreted as modified retromarginal teeth (scored 0). *Prodidomus*: a small mound might be a retromarginal relictual tooth (scored 1). *Lygromma*: close to promargin (scored 0). *Desognaphosa*: the small, most distal promarginal teeth is slightly central and might be a retromarginal displaced (scored 1). *Macerio*: one, very apical (scored 0). *Boliscus*: tooth almost on the furrow (scored 0).

49. Cheliceral retromarginal teeth origin: 0. Distinct (fig. 19H). 1. On common base (figs. 20G, 27E). COMMENTS: *Eresus, Stegodyphus*: not clear to which margin each tooth belongs (scored 01). *Nicodamus*: only one (scored -). *Cheiramiona*: three apical promarginals, including two small denticles (scored 0). *Cebrenninus*, *Epidius*, *Geraesta*: the two basal retromarginal on a common base, then one alone (scored 1).

50. Cheliceral denticles in furrow: 0. Absent. 1. Present, small denticles between promargin and retromargin (fig. 19B). COMMENTS: *Huttonia*: from Forster and Platnick (1984) (scored 0). *Castianeira*: the small prolateral not in furrow (scored 0). *Eilica*: no furrow, margins interpreted (scored 01). Cf. *Moreno* ARG: dubious, the two distal between retromargin and furrow (scored 01). *Pseudolampona*: the promarginal teeth are not well aligned, and the retromargin is well advanced anteriorly (scored 0).

51. Promargin cheliceral whisker setae: 0. Absent (fig. 18G). 1. Present, at least one (figs. 22D, 26D, 25G). On the anterior face of the chelicera, the whisker setae occur as a group (fig. 22D) or line (fig. 26D) more proximal to the rake, although in some groups only the escort seta remains (fig. 25G). The retromarginal whisker setae are more loosely defined; those near the base of the fang are similar to the promarginal ones, but the group often extends farther on the posterior side, and the setae become gradually thinner, straight, and less barbed (figs. 21D, 22F). Some Eutichuridae have a group of whisker setae near the retromarginal teeth (fig. 21A–C). Posterior whisker setae were tentatively scored in the dataset but not considered as an active character.

52. Promarginal escort seta: 0. Absent (figs. 19E, 20E, 21E, 22E, 23C). 1. Present (figs. 19F, H, 25G, 27C). The fluffy escort setae were used recently as characters for dionychans in the promargin (Bosselaers and Jocqué, 2002: char. 79; Platnick, 2000: char. 13) and entelegynes in the retromargin (Griswold et al., 2005: char. 34). Here I recorded the escort setae in both margins, but because both setae seem to vary coordinately, only the prolateral seta was retained as an active character for the analysis. The only cases where prolateral and retrolateral escort setae do not vary coordinately are also of dubious homology, with all retrolateral setae very small. COMMENTS: *Huttonia*: from Forster and Platnick (1984). *Homalonychus*: not so plumose but similar in shape (fig. 19E) (scored 0). *Corinna*, *Falconina*: short (scored 1). *Medmassa*: several setae of intermediate shape (scored 01). *Xenoplectus*: the retrolateral one seems also to be there, but very short (scored 1). *Gnaphosa*: present but reduced (fig. 27F) (scored 01). *Camillina*: promarginal and retromarginal short (scored 1). *Prodidomus*: the prolateral one not considered homologous (scored 0). *Lygromma*: the retrolateral one short but distinct (scored 1). Cf. *Moreno* ARG, *Lampona*, *Lamponella*, *Pseudolampona*, *Legendrena*, *Cithaeron*, *Fissarena*, *Doliomalus*, *Platyoides*, *Amaurobioides*: retrolateral seta reduced (fig. 26G). *Platyoides*: a few small ones (scored 0). *Vectius*: posterior setae broken (scored 1). *Austrachelas*: a series of large, bent setae on promargin (fig. 26D) (scored 1). *Meedo*, *Neato*: the retrolateral seta shorter, curved (scored 1). *Eusparassus*: one on retromargin, several on promargin, but none especially larger (scored 0). *Petrichus*: there are some longer setae, but not plumose (scored 0). *Epidius*: setae notably similar to those of *Cebrenninus* and *Geraesta* (scored 0). *Geraesta*, *Stephanopis ditissima*: a bunch of long setae, but all looking similar to each other (fig. 22E) (scored 0). *Xysticus*: might be intermediate (scored 0).

53. Cheliceral promarginal macrosetae: 0. Absent. 1. Present (figs. 18C, 22G), including "peg teeth" (see char. 54). COMMENTS: *Rastellus*: the large rastellum seta on ectal position, not on the promargin (fig. 25C) (scored 0). *Stephanopis ditissima*, *Xysticus*: the thick curved setae with barbs at tip are rake setae (scored 0). *Boliscus*: three short macrosetae, basal to the series of rake setae and slightly out of rake line (scored 1). *Tmarus*: only rake setae with distal barbs (fig. 23D) (scored 0).

54. Cheliceral peg teeth: 0. Absent. 1. Present. Peg teeth are short macrosetae with blunt tip, found in the cheliceral promargin of palpimanoids. In the taxa scored here, the peg teeth are always accompanied by a group of proximal macrosetae (fig. 17E). Here the peg teeth are more narrowly defined than in Forster and Platnick (1984), Platnick and Shadab (1993), and Griswold et al. (2005:

char. 41). For the tapering macrosetae found in *Mimetus*, see character 53.

55. Promargin rake setae basal barbs: 0. Small barbs or smooth. 1. Comb of thick barbs. Only in *Copa* in this dataset (fig. 20D), but present also in other castianeirines (Charles Haddad, personal commun.).

56. Cheliceral promarginal pronounced mound: 0. Absent. 1. Present (figs. 18E, 23C, F, 24C–E). 2. Mound plus dark long tooth (fig. 21F–H). States are ordered. This mound was discussed by Homann (1975) and is present in some thomisids as well (figs. 23F, 24C–E) as in philodromids. Immediately basal to the mound, philodromids have a black, elongate tooth (fig. 21G, H). The mound is seemingly mechanically correlated with the short fangs, as it also appears in *Filistata* (fig. 18E), *Mimetus*, and most Zodariidae. COMMENTS: *Filistata*: in the form of a membranous extension (fig. 18E) (scored 1). *Cybaeodamus*: two small dark teeth, but separated from the mound and not longitudinally oriented (scored 1). *Homalonychus*: just a slightly elevated ridge (scored 0). *Oxyopes*: intermediate, also similar tooth (scored 012). *Petrichus*: tooth not particularly dark (scored 2). *Aphantochilus*: also discussed in Homann (1975) (scored 1).

57. Cheliceral retromarginal pronounced mound: 0. Absent (fig. 23B, E). 1. Present, with a brush of setae. In the thomisids *Strophius* and *Aphantochilus* the retromarginal setae are grouped on a lobe similar to the one on the promargin (fig. 24F, G). COMMENTS: *Cryptothele*: only a brush of setae, no mound (scored 0).

58. Fang base and shaft relative sizes: 0. Shaft longer or same as base (figs. 17F, 19I, 25F, 26H, 27A). 1. Shaft shorter than base (fig. 19D). Only observed in the extremely reduced fangs of *Zodarion*, no terminal in this dataset has this condition. The shaft of the fang is often marked by a sudden constriction, bears longitudinal ridges, and an internal serrula. COMMENTS: *Desis*: very long base, about the same as shaft (scored 0). *Cryptothele*: about as long as base; fang articulation looks stiff, nonmovable (scored 1). *Storenomorpha*: cheliceral gland well separated from fang tip (scored 1). *Eilica*: shaft without longitudinal striae (scored 0). *Rastellus*: the fang has a large base seemingly without much movement (fig. 25D) (scored 0). *Ciniflella* ARG: shaft with few longitudinal striations (scored 0). *Strophius*: fang tips pointing anteriorly (scored 0).

59. Fang shaft serrula: 0. Present (figs. 26H, I, 27H). 1. Absent (figs. 26F, 27A). COMMENTS: *Uliodon*: few basal teeth (scored 0). *Acanthoctenus*: about seven basal teeth (scored 0). *Ctenus*: from stereomicroscope (scored 1). *Senoculus*: with large teeth (scored 0). *Creugas*: basal teeth (scored 0). *Brachyphaea*: seemingly absent, examined with stereomicroscope (scored 1). Cf. Liocranidae LIB: at least at the base (scored 0). Cf. Gnaphosoidea TEX: long serrula (scored 0). *Doliomalus*, *Platyoides*, *Rastellus*, *Selenops*: just a few teeth at the base (scored 0). *Hovops*: not SEM, the stereomicroscope shows just a few teeth at the base, as in *Selenops* (scored 0). *Anyphops*: basal serrula, seen with stereomicroscope (scored 0).

60. Plagula ventralis: 0. Absent. 1. Present (fig. 16B, D). Homann (1985) stated that the plagula ventralis is unique to Tetrapulmonata. According to Dunlop (1996) it is not present in all Araneae. See also Giribet et al. (2001) and Shear et al. (1987). No terminal in this analysis is proven to miss the plagula ventralis, which seems to be present throughout Araneomorphae as well. COMMENTS: *Oecobius*: seems absent in the clove oil preparation (scored ?). *Dictyna*: the clarification with clove oil shows the plagula ventralis as the sclerite where the fang flexor attaches, then transmitting by a short tendon to the fang (scored 1).

61. Venom gland: 0. Present (fig. 15A). 1. Absent. In this dataset only *Uloborus* is known to lack venom glands. In many cases the gland could be observed during the dissection of chelicerae for SEM (fig. 15A). A few scorings of outgroups were taken from Millot (1931b, 1933a–c), who made carapace sections to study the midgut diverticula of spiders, and from Forster (1955) and Forster and Platnick (1984). COMMENTS: *Eriauchenius*: from Petrunkevitch (1939) (scored 0).

62. Venom gland placement: 0. Limited to chelicerae. 1. Extending into carapace (fig. 15A). Hypochilids have venom glands confined inside the paturon; all other araneomorphs with venom glands, have them extending into the carapace (see Griswold et al., 2005: char. 52).

COMMENTS: *Hypochilus*: from Petrunkevitch (1933), Millot (1933b), Marples (1968) (scored 0). *Filistata*, *Eresus*, *Oecobius*, *Araneus*, *Dictyna*, *Zoropsis*: from Millot (1931a, 1933a–c), who made sections to study the midgut diverticula (scored 1). *Thaida*: after *Austrochilus* from (Marples, 1968) (scored 1). *Uloborus*: from Millot (1931a) (scored -). *Huttonia*: from Forster and Platnick (1984) (scored 1). *Eriauchenius*: from Petrunkevitch (1939) (scored 1). *Megadictyna*: from Forster (1970), Harvey (1995, reported as general for Nicodamidae) (scored 1). *Nicodamus*: Harvey (1995, reported as general for Nicodamidae) (scored 1). *Senoculus*: one specimen dissected (preparation MJR-953), but I cannot see the helicoidal muscles (scored 1). *Hortipes*: short gland, half endocheliceral (scored 1). *Ammoxenus*: from Petrunkevitch (1933) (scored 1). *Philodromus*: from preparation MJR-758 (scored 1).

63. Intercheliceral articulation: 0. Membranous movable. 1. Sclerotized stiff (figs. 7D, 18D). COMMENTS: *Eresus*: membranous articulation more sclerotized in the middle (scored 0). *Mimetus*: the articulation is stiff, not membranous, with very limited movement (fig. 7D) (scored 1). *Huttonia*: hard to move, intercheliceral sclerite in anterior position, midline very tight (scored 01). *Strophius*: articulation well advanced, flexible with some mobility (scored 0). *Aphantochilus*: articulation advanced, powerful, flexible area forming a sclerotized lobe, still some mobility (fig. 14G) (scored 01).

64. Intercheliceral sclerite: 0. Present, an elongate piece at the posterior end of cheliceral articulation, usually with a small protuberance (figs. 16A, 25A, 26J). 1. Absent, posterior end of cheliceral articulation without sclerite, or just a faint sclerotization. The intercheliceral sclerite was first noted by Wanless (1982) while revising the salticid genus *Cocalodes* and *Allococalodes*, whose males have such sclerites prolonged into a long, anteriorly directed horn between the chelicerae (see also Maddison, 2009: fig. 9). The same sclerite was also described by Platnick (2000: 15, fig. 8) as "posterior chilum, a narrow sclerite situated between the bases of the chelicerae." COMMENTS: *Filistata*, *Mimetus*: not applicable when chelicerae fused (scored -). *Eresus*: triangular, with branches on chelicerae concavities (scored 0). *Oecobius*: observed with compound microscope (scored 0). *Cryptothele*: not dissected, but no sclerotization evident (scored 1). *Huttonia*: anteriorly placed! (scored 0). *Senoculus*: a small sclerotized hump (scored 01). *Centrothele*: from Platnick (2000) (scored 0). *Petrichus*: slightly wider than in other terminals (scored 0). *Strophius*: only a thin sclerotized line remains (scored 1). *Cocalodes*: normal elongate with small protuberance, not reduced as in advanced salticids, male with a long horn! (scored 0).

65. Intercheliceral sclerite configuration: 0. Elongate piece. 1. Triangular piece plus separate posterior bar (Wood et al., 2012: fig. 5a, f). This state occurs only in *Eriauchenius* in this dataset.

MOUTHPARTS: LABRUM, LABIUM, AND ENDITES

The labrum bears an anterior sclerite, the labral tongue (fig. 28B). Because of confusion with previous ambiguous usages, this new term was coined by Miller et al. (2009), and corresponds to "labral flap" of Lopardo and Hormiga (2008) and "labral sclerite" of Kropf (1990). The palpal coxae are expanded in araneomorph spiders, forming the endites, bearing a distal-lateral serrula. The maxillary gland discharges through a field of pores, usually on the dorsal surface of the endite, but sometimes on its medial surface. This pore plate is also known as "gnathocoxal gland" or "sieve plate." The labium (fig. 28A) is articulated or fused to the distal margin of the sternum.

66. Lateral labral extensions: 0. Absent (fig. 28C). 1. Present. Only *Eriauchenius* in this dataset (fig. 28F). The lateral labral extensions were described by Forster and Platnick (1984) as a synapomorphy of archaeids and the mecysmaucheniids. Schütt (2003: char. 22) used the term "labral appendage" for each of these protuberances. COMMENTS: *Filistata*: provisionally scored from *Kukulcania* (scored 0).

67. Labium fusion with sternum: 0. Free from sternum (figs. 29G, 31D). 1. Fused to sternum (fig. 29B). COMMENTS: *Hypochilus*: fused, but separated by a depression (scored 1).

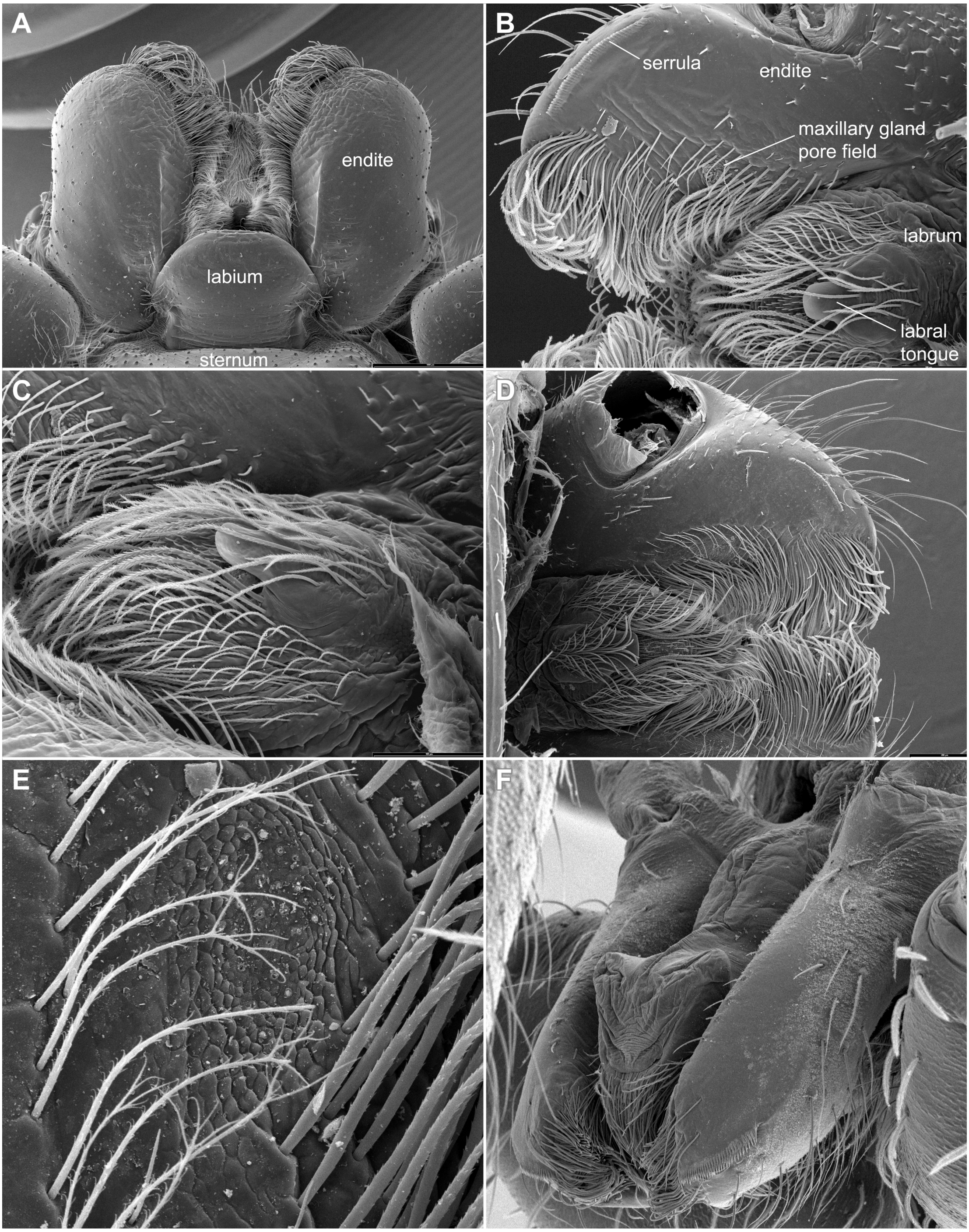

A
endite
labium
sternum
B
serrula
endite
maxillary gland
pore field
labrum
labral
tongue
C
D
E
F

Fig. 28. Mouthparts of female. **A.** *Eusparassus* cf. *walckenaeri* (Sparassidae). **B.** *Pronophaea proxima* (Corinnidae). **C.** Same, dorsal-lateral view. **D.** *Falconina gracilis* (Corinnidae). **E.** Same, detail of maxillary gland. **F.** *Eriauchenius workmani* (Archaeidae).

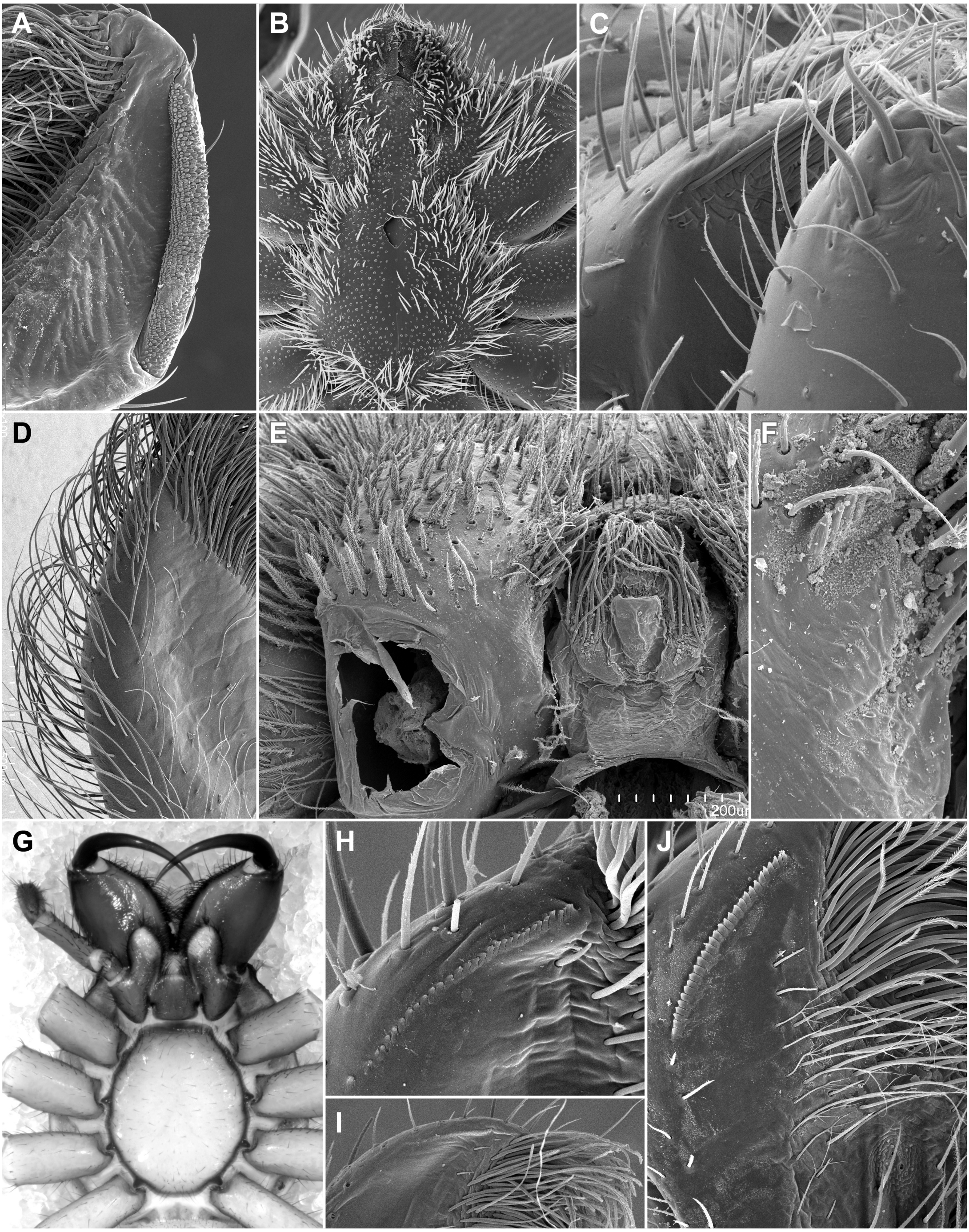


Fig. 29. Mouthparts of female (except C, immature). **A.** *Hypochilus pococki* (Hypochilidae). **B.** *Kukulcania hibernalis* (Filistatidae). **C.** *Cryptothele alluaudi* (Zodariidae). **D.** *Desis formidabilis* (Desidae), apical. **E.** *Ammoxenus coccineus* (Ammoxenidae). **F.** Same, close-up of serrula. **G.** *Platyoides walteri* (Trochanteriidae). **H.** Same, close-up of serrula. **I.** *Doliomalus cimicoides* (Trochanteriidae). **J.** *Paravulsor* sp. (Miturgidae).

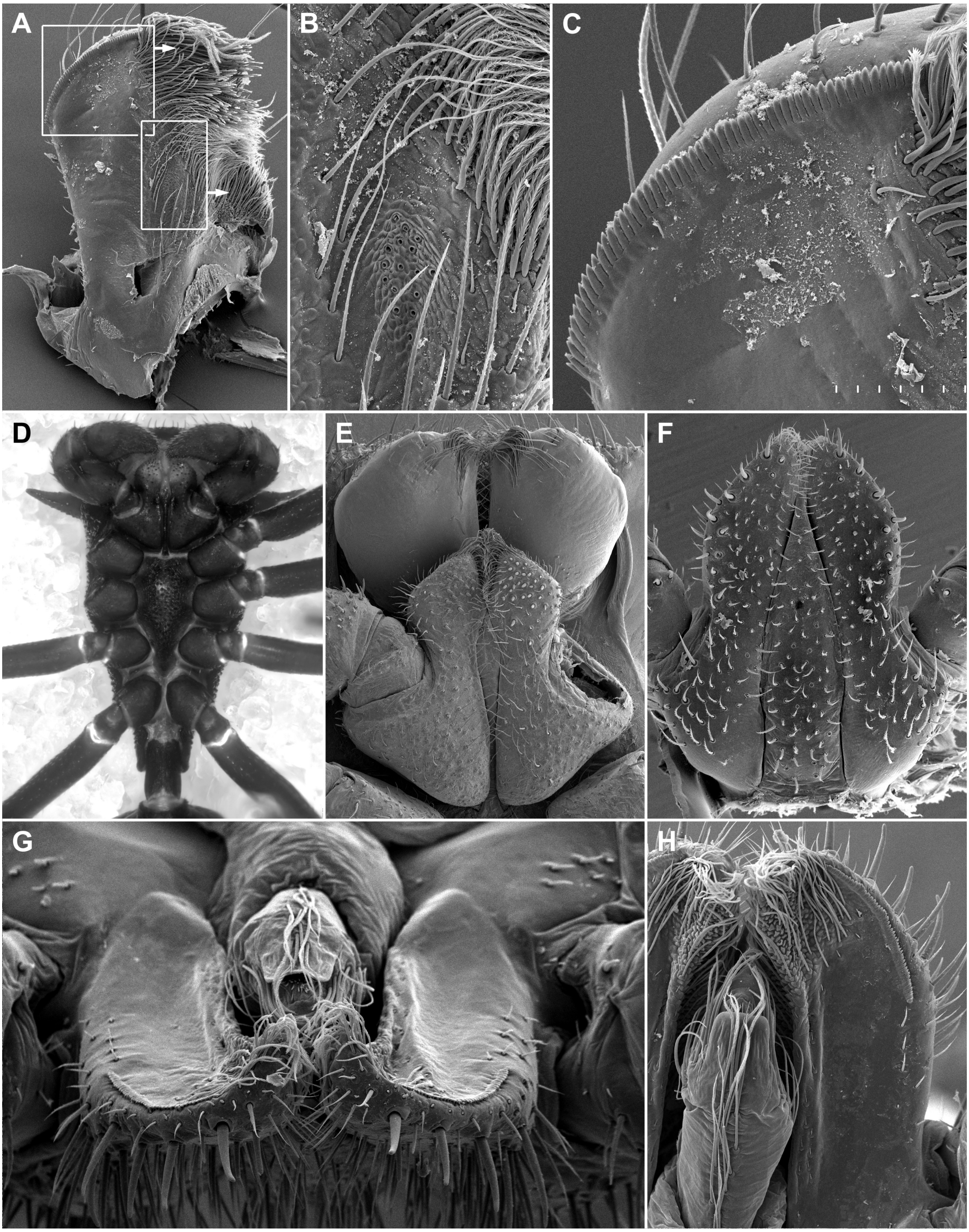


Fig. 30. Mouthparts of female (except D, male). **A.** *Gayenna americana* (Anyphaenidae), marked insets shown on B and C. **B.** Same, close-up of maxillary gland. **C.** Same, close-up of serrula. **D.** *Aphantochilus rogersi* (Thomisidae), cephalothorax ventral. **E.** *Aphantochilus rogersi* (Thomisidae). **F.** *Strophius albofasciatus* (Thomisidae). **G.** Same, frontal. **H.** Same, dorsal.

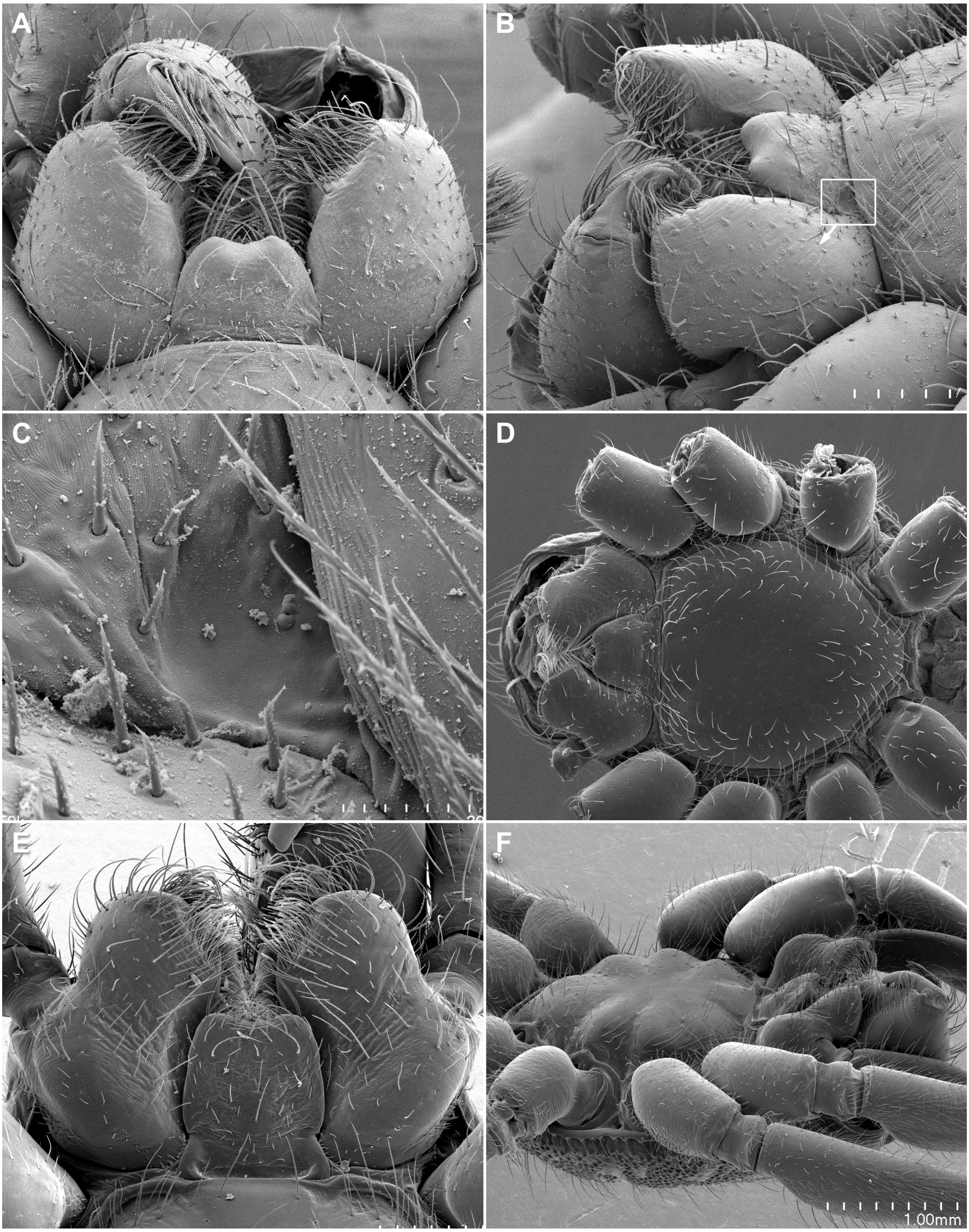


Fig. 31. Mouthparts of female. **A.** *Phrurotimpus alarius* (Phrurolithidae). **B.** Same, lateral-ventral, marked insets shown on C. **C.** Same, detail of labial pit. **D.** Trachelidae ARG. **E.** *Sesieutes* sp. (Liocranidae). **F.** Same, carapace lateral-ventral.

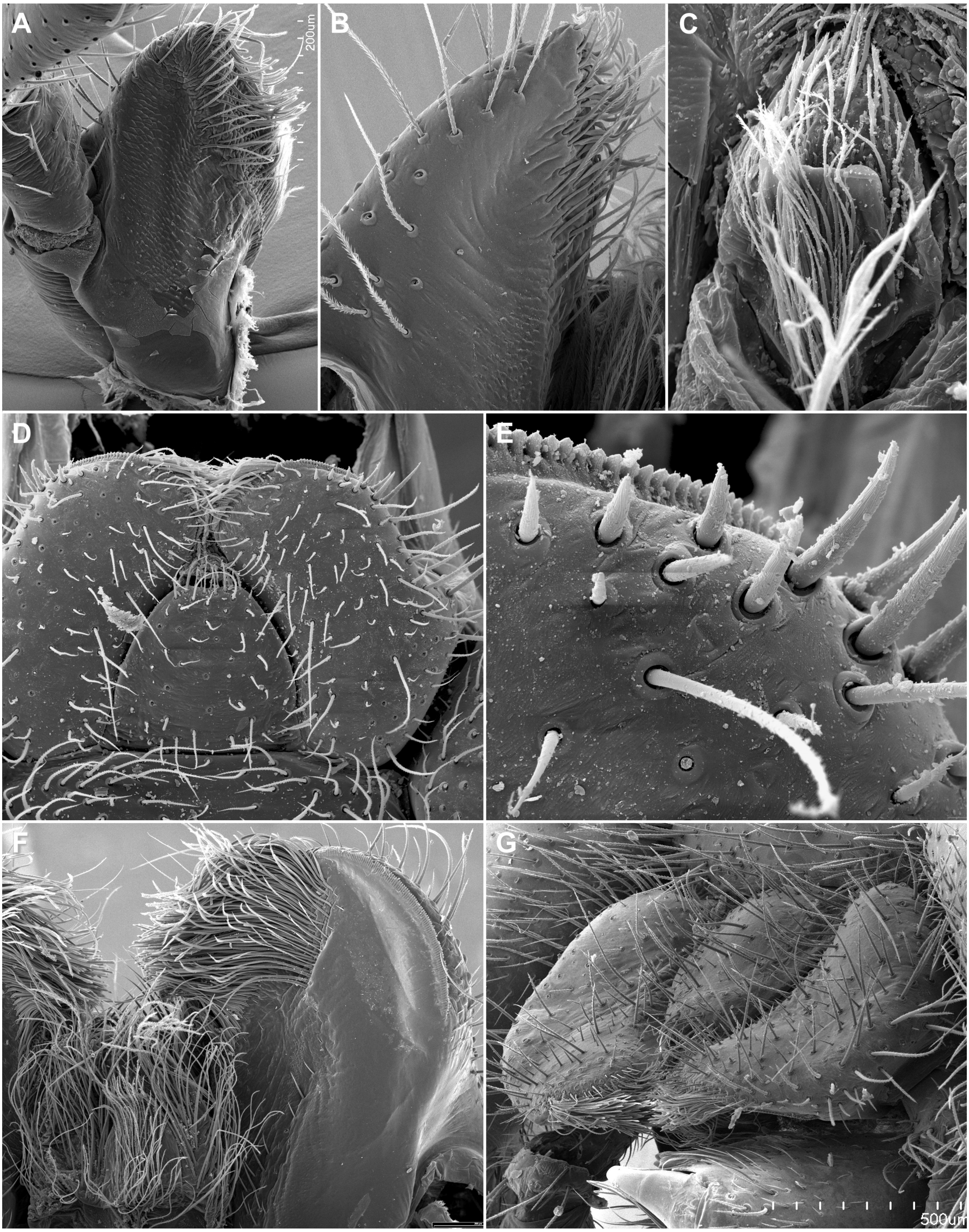


Fig. 32. Mouthparts of female. **A.** *Neozimiris pubescens* (Prodidomidae). **B.** Same, close-up apical. **C.** *Eilica* sp. (Gnaphosidae), labrum. **D.** Same, endites and labium. **E.** Same, detail of serrula, and tip of endite, ventral view. **F.** *Apodrassodes quilpuensis* (Gnaphosidae). **G.** *Gnaphosa sericata* (Gnaphosidae).

68. Labium length/width ratio: 0. Longer than wide or about equal width and length (fig. 31E). 1. Wider than long (fig. 31A). COMMENTS: *Oecobius*, *Uloborus*, *Dictyna*, *Pimus*, *Cryptothele*, *Homalonychus*, *Vulsor*, *Castianeira*, *Copa*, *Medmassa*, *Brachyphaea*, *Olbus*, *Agroeca*, *Liocranum*, *Neoanagraphis*, *Phrurolithus*, *Drassinella*, *Sesieutes*, *Prodidomus*, *Neozimiris*, *Lygromma,* cf. *Moreno* ARG, *Legendrena*, *Trachycosmus*, *Fissarena*, *Ammoxenus*, *Cithaeron*, *Philodromus*, *Tibellus*, *Selenops*, *Geraesta*, *Xysticus*: about as wide as long (scored 0). *Lamponella*, *Pseudolampona*: labium triangular (scored 0). *Meedo*: About as wide as long. I cannot see the peculiar shape described by Platnick (2002) (scored 0). *Phrurotimpus*: note the basal depressions with a pore, as in Theridiosomatidae (fig. 31B, C) (scored 1). *Neato*: ‘‘bipartite’’ in Platnick (2002), here interpreted as bent over a median transverse line (scored 1).

69. Labium fusiform: 0. Absent, the labium may be trapezoidal or elongate (fig. 30F), but without reaching the extreme shape of aphantochilines. 1. Present, the labium is extremely long and thin, very narrow at the base, with the posterior end of maxillae adjacent to each other (fig. 30D, E). COMMENTS: *Strophius*: elongate, but not fusiform (fig. 30F) (scored 0).

70. Endites obliquely depressed: 0. Absent (figs. 28A, 30F). 1. Present (figs. 6C, E, 31F, 32G). This traditional character for Gnaphosoidea was recently used in cladistic analyses by Platnick (2000: char. 10; 2002: char. 2) and Bosselaers and Jocqué (2002: char. 83). They mention that the character is also present in some outgroups as well (e.g., *Orthobula*, fig. 6C). COMMENTS: *Eresus*: depressed, although with different shape than in gnaphosoids (scored 1). *Uloborus*: all median area depressed (scored 0). *Mimetus*: basal depression, not clearly defined as oblique (scored 01). *Cyrioctea*: perhaps very slightly (scored 0). *Cybaeodamus*: might be intermediate (scored 0). *Senoculus*: slightly depressed, more markedly so on males (scored 01). *Liocranum*: intermediate in female, male a little more evident (scored 01). *Xenoplectus*: not markedly depressed (scored 1). *Phrurolithus*: very slightly depressed, as in *Phrurotimpus* female (scored 0). *Phrurotimpus*: very slightly depressed on female (fig. 31B), more markedly so on male (scored 01). *Otacilia*: on males more markedly depressed (scored 01). *Oedignatha*: depressed according to Robert Raven (in litt.), too faint depression for my criterion (scored 0). *Anagraphis, Pseudolampona*: very slightly depressed (scored 0). *Meedo*: very slight basal depression (scored 01). *Trachycosmus*: contra Platnick (2002) (scored 0). *Ammoxenus*: the basal area is globose, the apical very small (scored 1). *Syspira*: depressed in other species from Dominican Republic (scored 0). *Heteropoda*: Just slightly depressed. There is a conspicuous oblique glabrous area (scored 0). *Tmarus*: might be intermediate (scored 1).

71. Endite ventral distal macrosetae: 0. Absent. 1. Present, the endite has macrosetae on the ventral surface of its distal half (fig. 30D–G). A synapomorphy of *Aphantochilus* and *Strophius*, also found in the gnaphosid *Eilica*. Many mygalomorphs also have blunt macrosetae (cuspules) on their mouthparts (Raven, 1985).

72. Maxillary gland pore field: 0. Absent. 1. Present, a patch of pores on the dorsal side of the endite (figs. 28D, 30A, B, 32C). This character has been introduced to collect observations on this easily overlooked structure. In several families the gland openings are on the mesal surface of the endite facing the labrum (fig. 32C), hence SEM examination of the mouthparts is not conclusive to indicate absence of gland outlets. In this dataset, and so far in the literature, there are no clearly documented absences of maxillary gland outlets in spiders. COMMENTS: Trachelidae ARG: perhaps only two pores (scored ?). *Camillina*: not seen (scored ?). *Eilica*: in mesal furrow (scored 1). *Neozimiris*: small round patch (scored 1). *Lampona*: from Platnick (2000: fig. 17). *Ammoxenus*: from Petrunkevitch (1933), but not seen in SEM (scored 1). *Griswoldia*: observed with stereomicroscope (scored 1). *Titanebo*: not visible in dorsal view (scored ?). *Thomisus*: in a small pit! (scored 1). *Strophius*: just a few pores (scored 1). *Cocalodes*: elongate patch at border of pilose area (scored 1). *Plexippus*: marginal (scored 1).

73. Endite dorsal setae: 0. Simple (fig. 32F). 1. Branched (figs. 28E, 29J). COM-

MENTS: *Centrothele*: from Platnick (2000: fig. 401) (scored 1). *Griswoldia*: observed with stereomicroscope (scored 1).

74. Serrula: 0. Present (figs. 29H, J, 30C, H). 1. Absent (figs. 29D, C, 32A, B). COMMENTS: *Cryptothele*: just a dark ridge (fig. 29C) (scored 1). *Brachyphaea*: *Andromma* sister to *Brachyphaea* in Bosselaers and Jocqué (2000), also with reduced serrula (scored 1). *Doliomalus*: only superficial traces of a single row serrula (fig. 29I) (scored 01). *Platyoides*: weak serrula (scored 0).

75. Serrula rows: 0. Multiple rows (fig. 29A). 1. Single row (figs. 29H, J, 30C, H).

76. Serrula width: 0. Wide bordering apex (fig. 30H). 1. Very short (fig. 29E, F). COMMENTS: cf. Liocranidae LIB: short, but not that short as in *Ammoxenus* (scored 0). *Desognaphosa*: short, but also narrow endite (scored 01). *Ammoxenus*: medial (scored 1). *Zora*: subapical (scored 1).

FEMALE PALP

The female palp lacks a metatarsus or a metatarsal distal stopper (fig. 33A, B). The articulation between tarsus and tibia has two dorsal condyles (fig. 33B), similarly as in the leg tibia-metatarsus joint. The tarsus has a tarsal organ, and bears one claw (fig. 33C), flexibly articulated on a claw lever, similarly as occurs with the superior leg claws. Similarly as in the legs, there is one tarsal slit sensillum at each side near the insertion of claw lever. The ventral side of the palpal tarsus often has setae with aligned barbs (fig. 38D), reminiscent of the cheliceral promarginal rake setae.

77. Female palpal femoral thorns: 0. Absent (figs. 33A, 38A). 1. Present, prolateral near the proximal joint (fig. 33F). The femoral thorns are not perfectly correlated with the stridulatory ridges on chelicerae (char. 37). For example, the amaurobiid *Retiro* has femoral cusps but not cheliceral ridges, and the archaeid *Eriauchenius* apparently stridulates by scraping a series of bristles on metatarsus III against the cheliceral ridges (Millot, 1948). COMMENTS: *Huttonia*: one (fig. 33F) (scored 1). *Pimus*: a series of thorns, weaker on female (scored 1).

78. Female palpal tarsus scopula of tenent setae: 0. Tenent setae absent (figs. 34I, 39C). There may be setae with aligned barbs (figs. 33D, E, 38C, D), or macrosetae. 1. Scopula lateral and dorsal (fig. 34E–H). 2. Scopula ventral (fig. 36A, B). The philodromid *Titanebo* has a ventral scopula of tenent setae on the distal half of the female palpal tarsus. Scopular setae are identified by the tenent surface (see char. 161). Normally the scopular setae are absent in the palp. COMMENTS: *Huttonia*: lateral dense scopula of modified setae, not tenent (scored 0). *Pronophaea*: ventral setae short, with aligned barbs, as in apex of metatarsus IV (scored 0). *Camillina*: female palp observed with stereomicroscope (scored 0). *Paravulsor*: ventral thick, long, blunt setae (scored 0). *Philodromus, Tibellus*: coded separately as an apical tuft, see character 79 (scored 0). *Titanebo*: ventral scopula on distal half (scored 2). *Hispo*: chisel-shaped setae (scored 0).

79. Female palpal tarsus apical tenent tuft: 0. Absent. 1. Of pseudotenent setae with acute tip (figs. 34A–D, 35A–F). See definition of pseudotenent setae in character 163. 2. Of tenent setae with truncate tip (fig. 36B–E). See definition of tenent setae in character 163. This is a synapomorphy of Philodromidae, and also occurs in males (fig. 36G, F). The covariation in both sexes was documented in a separately scored, inactive character for the males. COMMENTS: *Cybaeodamus*: no SEM, similar to pseudotenent under the stereomicroscope, setae on legs with no expanded barbs (scored 01). *Meedo*: Platnick (2002) refers to a dense ventral scopula, but it is composed of stiff setae without tenent barbs (scored 0). *Paravulsor*: similar as in *Zora* (scored 1). *Xenoctenus*: scopula, not claw tuft (scored 0). *Austrachelas*: a few cylindrical setae at side of claw with a small tenent patch (fig. 40D, E) (scored 01). *Odo bruchi*: the scopula extends without transition to the sides of the claw (scored 0). *Geraesta, Boliscus*: perhaps pseudotenent (scored 01). *Titidius*: like pseudotenent but not with expanded barb tips (scored 0).

80. Blunt seta at side of palpal claw: 0. Absent. 1. Present. A synapomorphy of *Olbus* (Ramírez et al., 2001: fig. 14).

81. Female palpal tarsus tip with short macrosetae: 0. Absent. 1. Present. Used as a synapomorphy of Ammoxenidae by Platnick (2002: char. 25, figs. 3, 4), here also occurs in

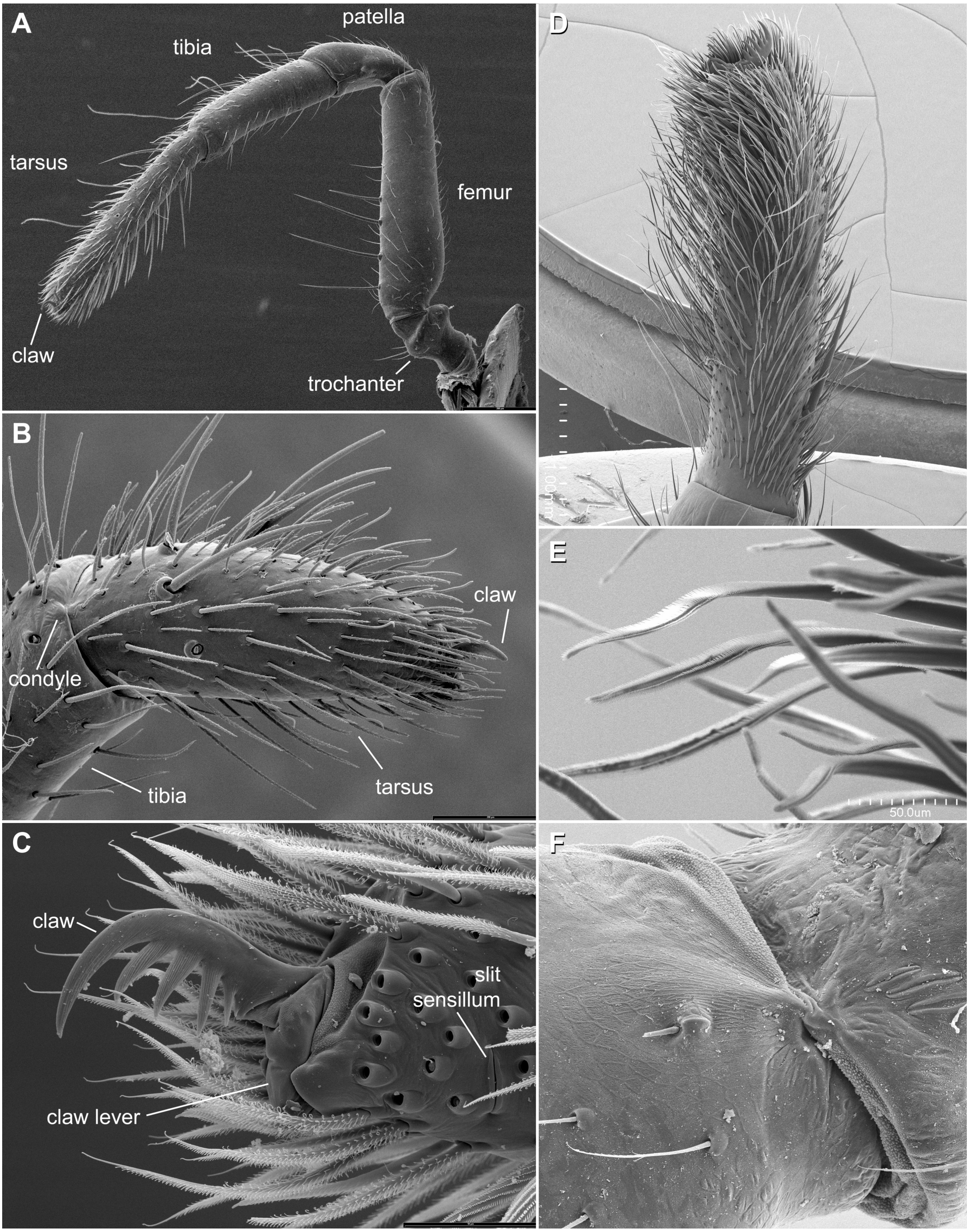

A
patella
tibia
tarsus
femur
claw
trochanter
D
1.00mm
B
claw
condyle
tibia
tarsus
E
50.0um
C
claw
slit
sensillum
claw lever
F

Fig. 33. Structures of female palp. **A.** *Teutamus* sp. (Liocranidae). **B.** *Doliomalus cimicoides* (Trochanteriidae). **C.** *Paravulsor* sp. (Eutichuridae). **D.** *Ctenus* cf. *crulsi* (Ctenidae). **E.** Same, detail of ventral apical setae. **F.** *Huttonia* sp. (Huttoniidae).

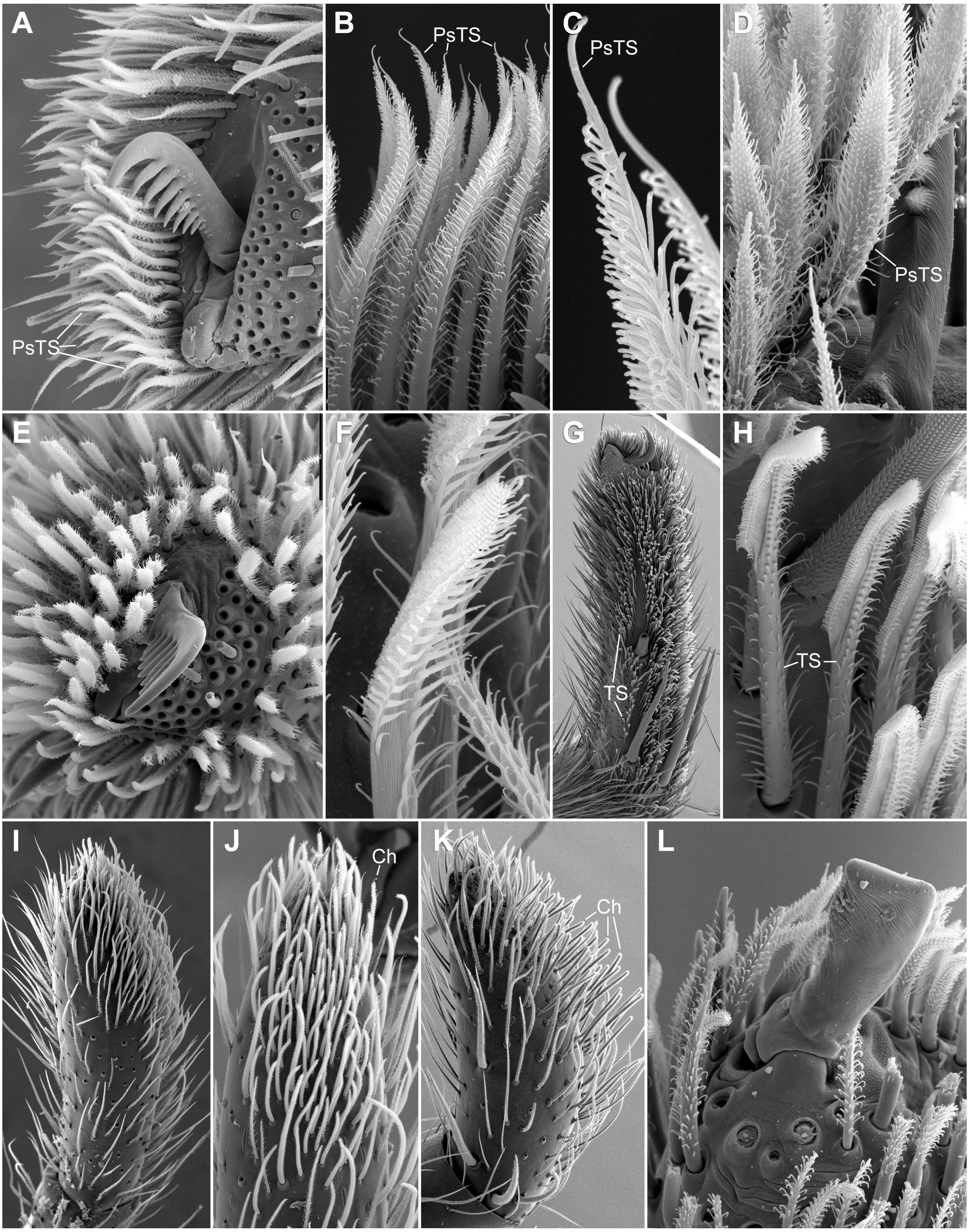


Fig. 34. Structures of female palp. **A.** *Miturga gilva* (Miturgidae), claw and apical setae. **B.** Same, detail of apical setae. **C.** Same, detail of setae tips. **D.** *Zora spinimana* (Miturgidae), claw and apical setae. **E.** *Odo bruchi* (Miturgidae), claw and apical setae. **F.** Same, detail of lateral-apical scopular setae. **G.** *Xenoctenus* sp. (Miturgidae), tarsus lateral. **H.** Same, detail of lateral scopular setae. **I.** Cf. Eutichuridae QLD (Eutichuridae?), tarsus lateral. **J.** Eutichuridae MAD (Miturgidae), dorsal chemosensory patch. **K.** *Malenella nana* (Anyphaenidae), tarsus lateral. **L.** *Lessertina mutica* (Eutichuridae), claw.

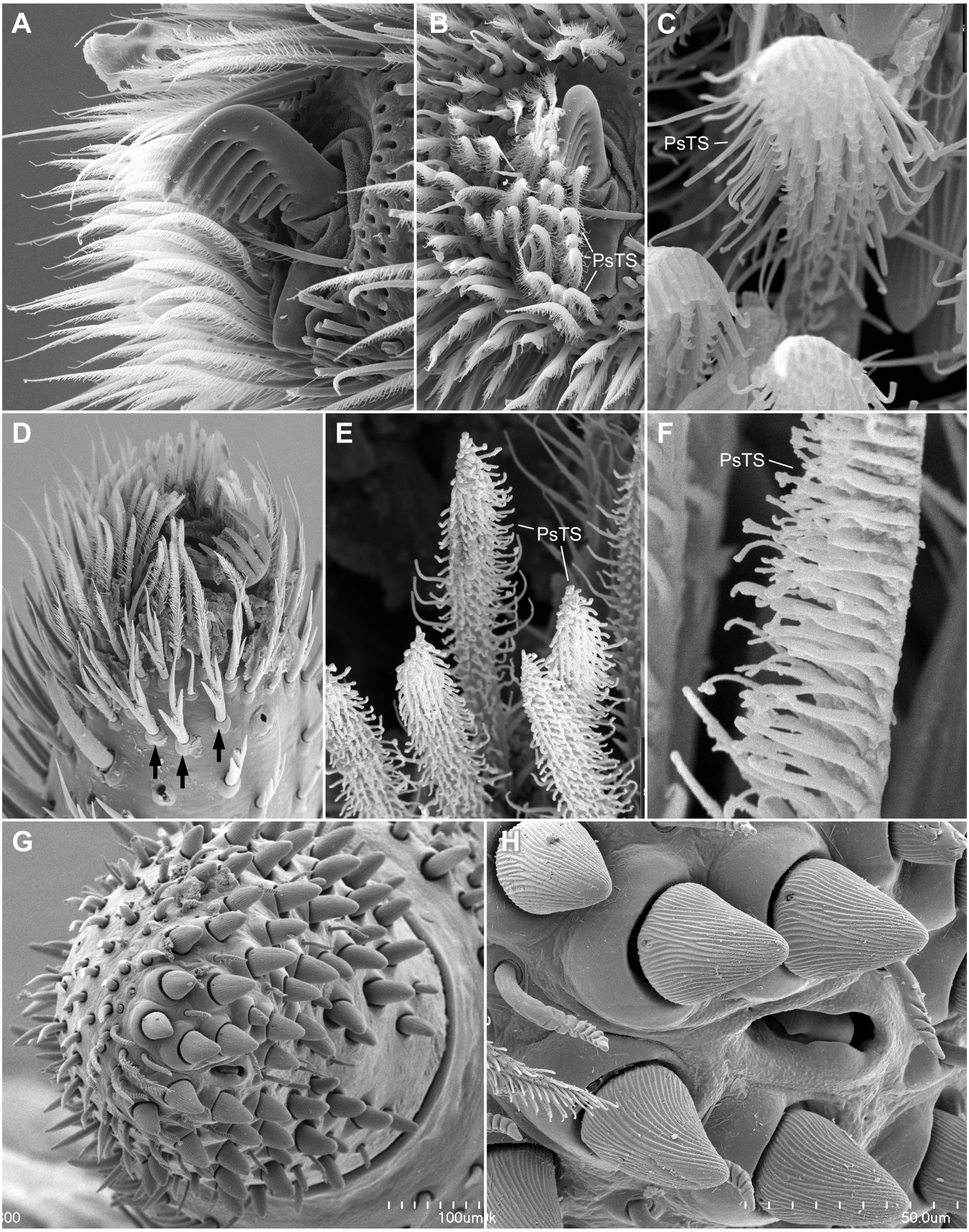


Fig. 35. Structures of female palp, Thomisidae. **A.** *Stephanopoides sexmaculata*, claw and apical setae. **B.** Same, apical. **C.** Same, detail of peudotenent setae. **D.** *Strophius albofasciatus*, arrows to serrate hairs. **E.** Same, detail of apical pseudotenent setae. **F.** Same, close-up of tenent barbs. **G.** *Aphantochilus rogersi*, apical. **H.** Same, relict of palpal claw and macrosetae.

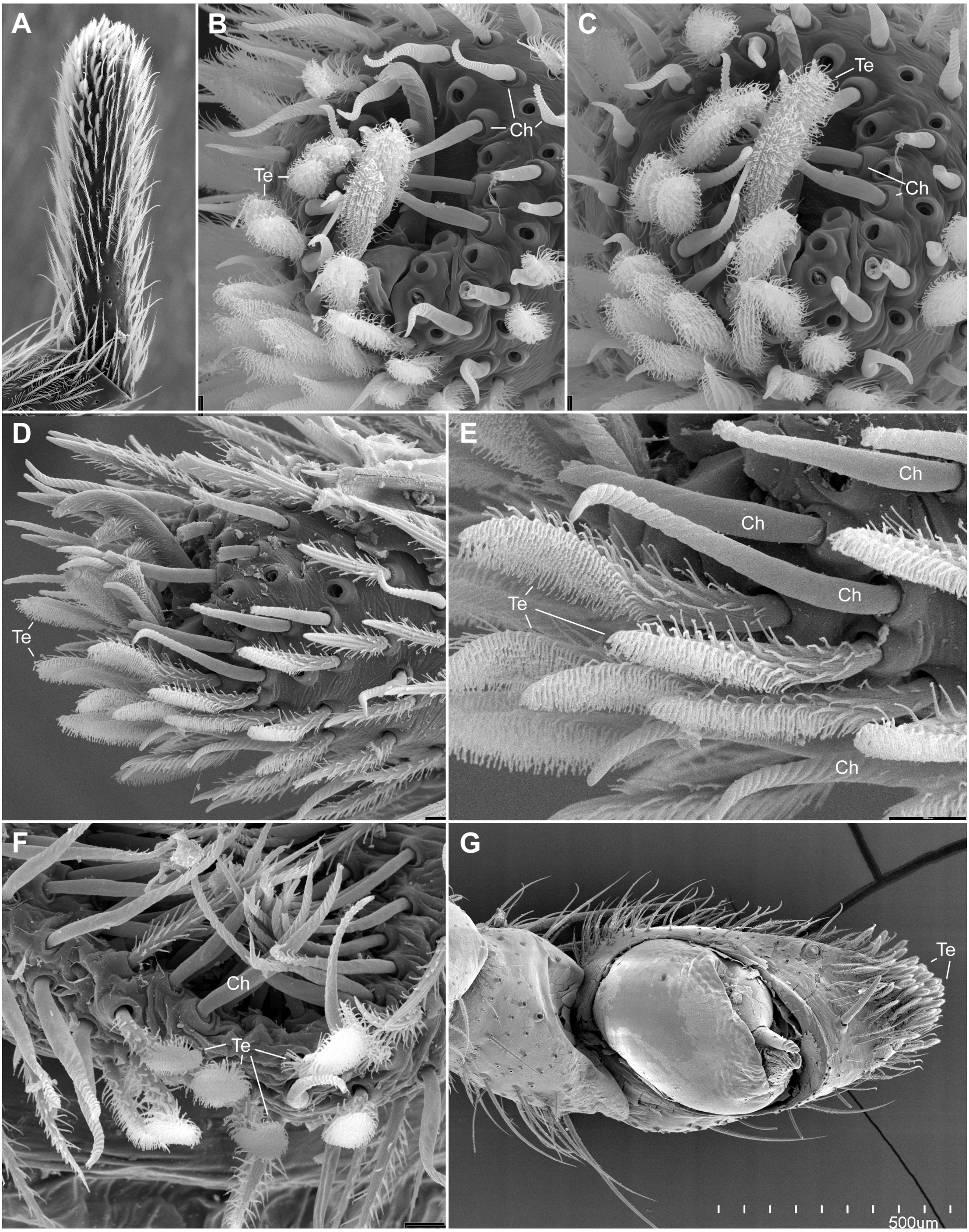

A
B
Ch
Te
C
Te
Ch
D
Te
E
Ch
Ch
Ch
Te
Ch
F
Ch
Te
G
Te
500um

Fig. 36. Structures of palps, Philodromidae. **A.** *Titanebo mexicanus,* female tarsus, retrolateral. **B.** Same, detail apical. **C.** Same, detail apical. **D.** *Petrichus* sp., female tarsal claw, retrolateral. **E.** Same, detail of tenent and chemosensory setae. **F.** Same, male cymbium tip, apical, tenent setae and chemosensory patch. **G.** *Tibellus oblongus* male palp, ventral view.

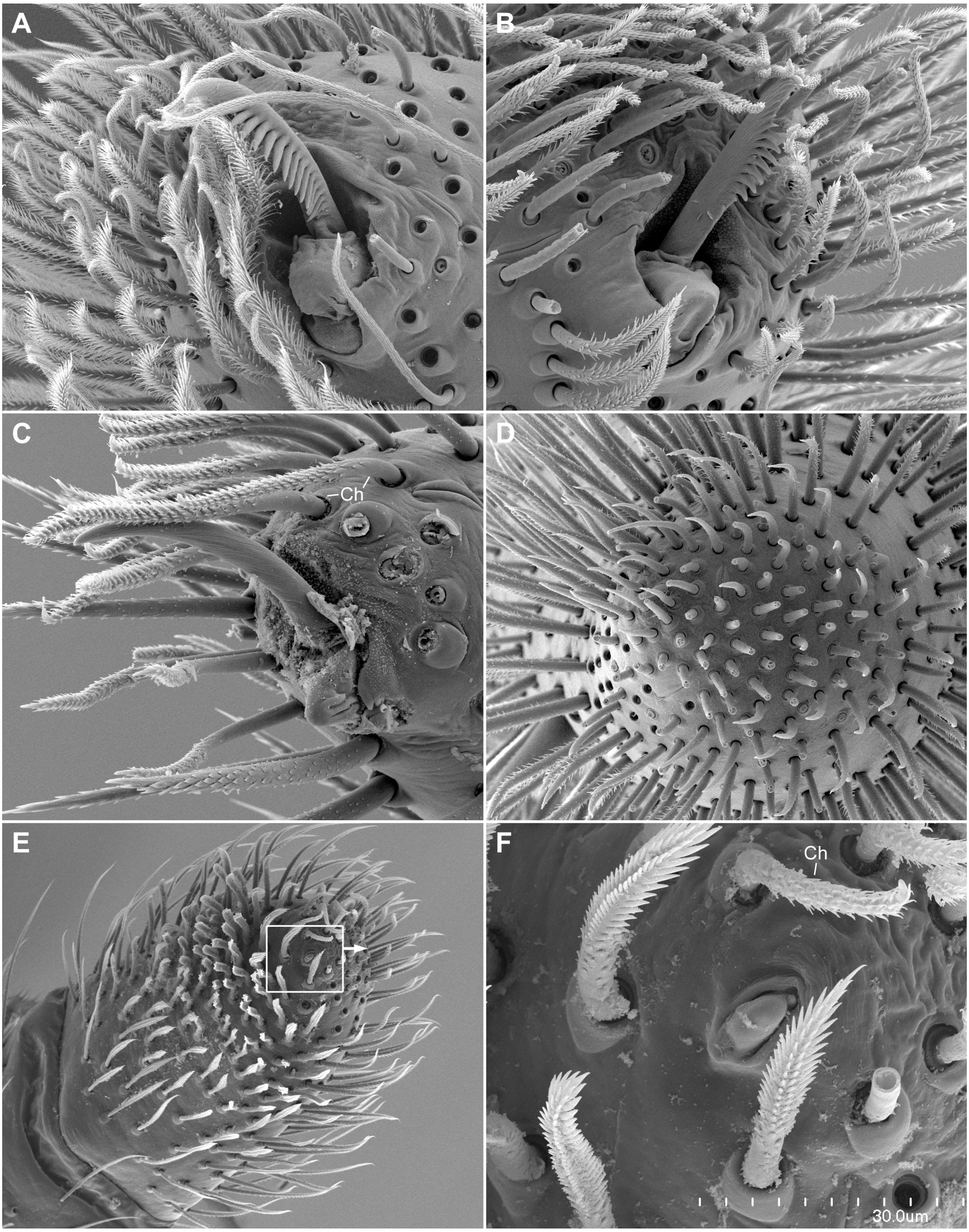


Fig. 37. Female palpal claws, Salticidae. **A.** *Portia schultzi*. **B.** *Holcolaetis* cf. *zuluensis*. **C.** *Lyssomanes viridis*. **D.** *Plexippus paykulli*, tip of tarsus. **E.** *Hispo* sp., inset enlarged in F. **F.** Same, detail of claw nubbin.

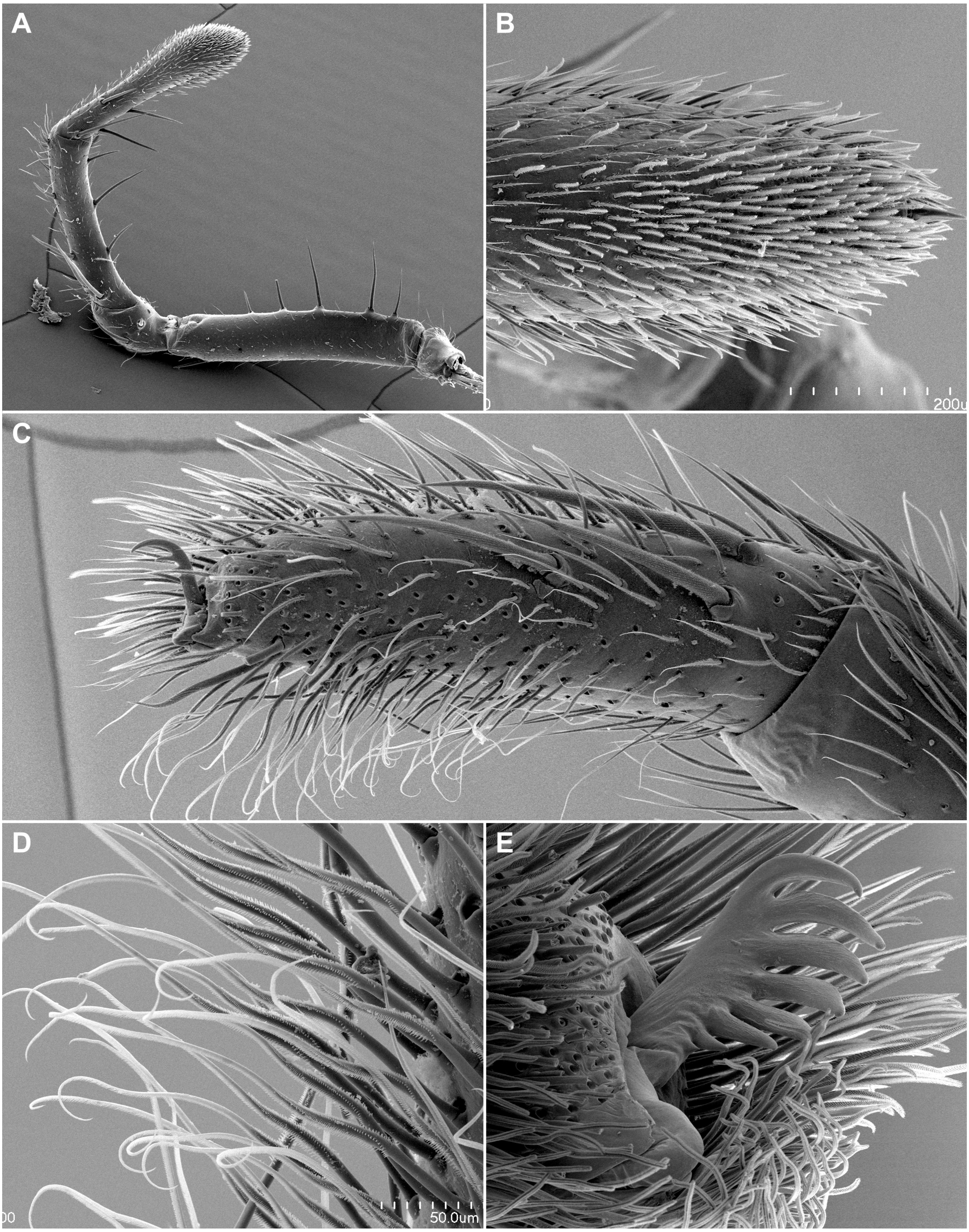


Fig. 38. Female palpal claws and setae. **A.** *Donuea* sp. ("Liocranidae") female **B.** Same, detail of dorsal chemosensory patch. **C.** Sparianthinae VEN (Sparassidae) female. **D.** Same, detail of ventral setae. **E.** *Heteropoda venatoria* (Sparassidae) female.

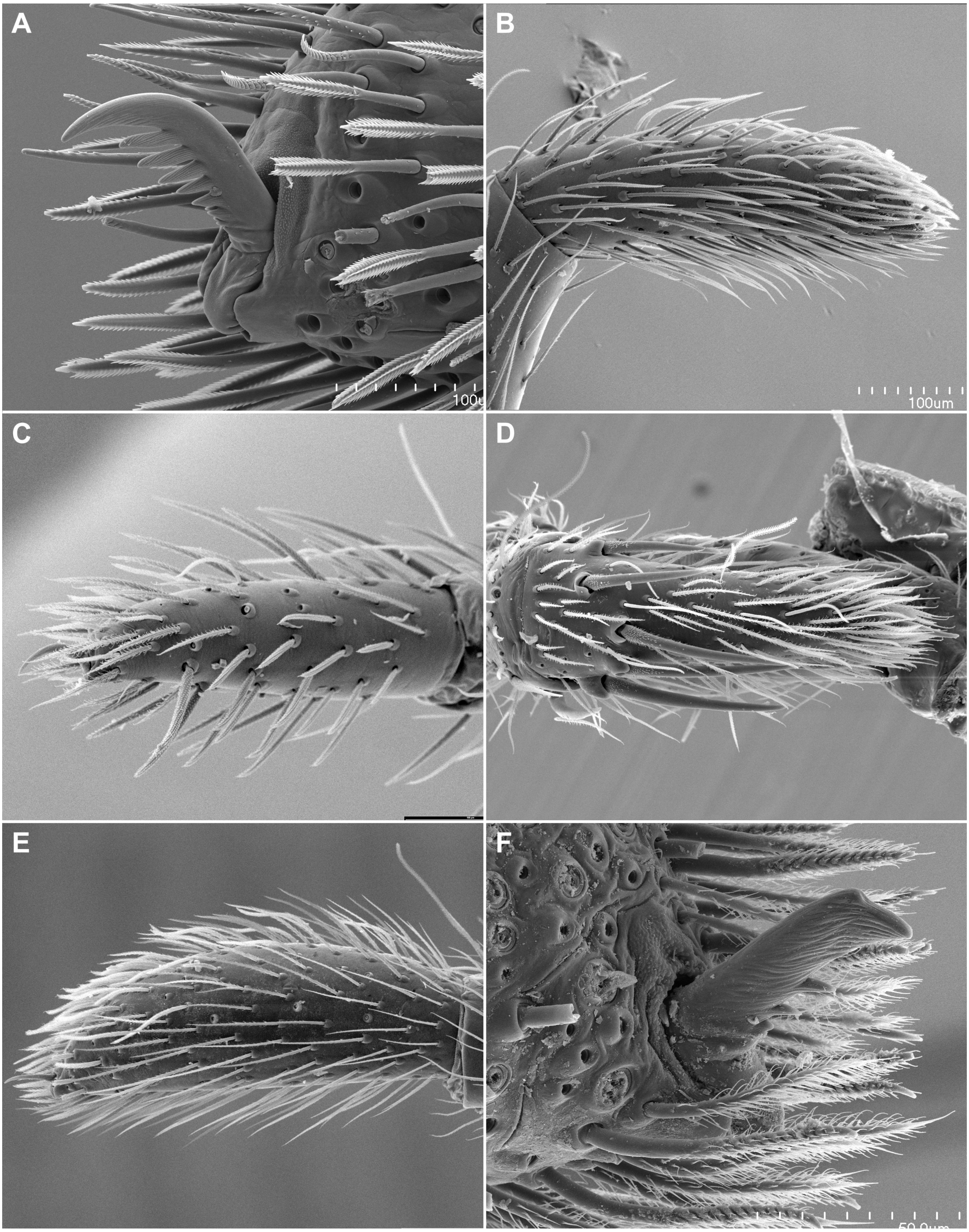


Fig. 39. Structures of female palp. **A.** *Corinna bulbula* (Corinnidae), claw. **B.** *Hortipes merwei* ("Corinnidae"), tarsus prolateral. **C.** *Apostenus californicus* (Liocranidae), tarsus retrolateral. **D.** *Xenoplectus* sp. ("Gnaphosidae") tarsus dorsal. **E.** Trachelidae ARG, tarsus retrolateral. **F.** *Trachelas mexicanus* (Trachelidae), claw.

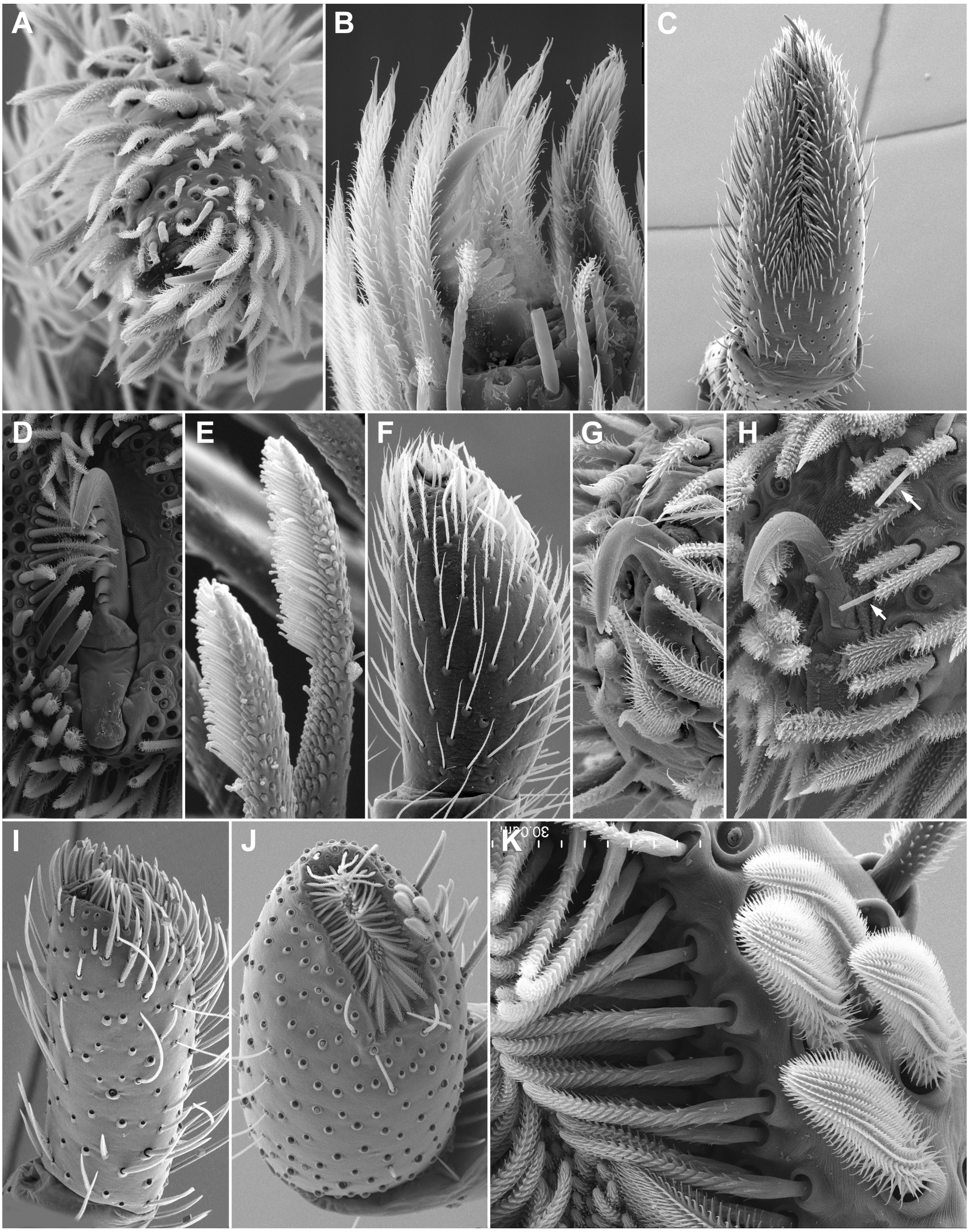


Fig. 40. Structures of female palp. **A.** *Rastellus florisbad* (Ammoxenidae), tarsus apical. **B.** Same, claw dorsal-retrolateral. **C.** *Meedo houstoni* (Gallieniellidae), tarsus dorsal. **D.** *Austrachelas pondoensis* (Gallieniellidae), claw apical. **E.** Same, detail of apical setae. **F.** *Lamponella brookfield* (Lamponidae), tarsus retrolateral. **G.** *Micaria fulgens* (Gnaphosidae), claw apical. **H.** *Lygromma* sp. (Prodidomidae), claw apical, arrows to setae with elongated, pore-bearing tube. **I.** *Neozimiris pubescens* (Prodidomidae), tarsus retrolateral-apical. **J.** *Prodidomus redikorzevi* (Prodidomidae), tarsus apical. **K.** Same, detail of apical setae.
"

Aphantochilus (fig. 35G, H). On close examination, the thick apical setae in *Rastellus* have acute tips with barbs (fig. 40A, B), perhaps a reversion within Ammoxenidae. COMMENTS: *Cryptothele*: not so short (scored 01). *Ammoxenus*: from Platnick (2002: figs. 3, 4). *Pseudocorinna*: a cuticular papilla close to palpal claw (scored 0). *Aphantochilus*: also on ventral side, note pores on macrosetae (fig. 35H).

82. Short medially thickened female palpal tarsus: 0. Absent. 1. Present (fig. 34K), an autapomorphy of *Malenella* (Anyphaenidae, Malenellinae) (Ramírez, 1995: char. 8; 2003: char. 31), also scattered in other terminals (figs. 39E, 40F). The palpal tarsi of clubionines and the eutichurid *Eutichurus* were scored as truncated by Silva Davila (2003: char. 118; see also Bonaldo, 1994: 104). Distally thickened palps are also somewhat truncated at the end (e.g., *Donuea*, fig. 38A), but there are too many intermediate conditions for a reliable scoring. I preferred to score here the extreme condition in *Malenella*, and a more qualitative character definition for the truncate tip (see char. 84). COMMENTS: *Donuea*: distally thick (fig. 38A) (scored 0). *Mandaneta*: slightly thickened, but apically (scored 0). *Pseudocorinna, Centrothele*: slightly thickened (scored 0). *Ammoxenus*: very short, conic (scored 0). *Stephanopis ditissima*: conic, flat (scored 0). *Prodidomus*, *Neozimiris*: ambiguous, because the tarsus is uniformly thick and short (scored 01). *Strophius*: conic (scored 0).

83. Female palpal tarsus dorsal chemosensory setae distribution: 0. Scattered. The chemosensory setae do not form a defined patch (fig. 39B, D). 1. In a defined patch (fig. 34J). COMMENTS: *Donuea*: many setae not forming a well-defined patch (fig. 38B) (scored 01). *Clubiona*, *Elaver*, *Donuea*, *Falconina*, *Paradiestus*, *Paccius*, *Hortipes*, *Eilica*, *Lessertina*, *Miturga* cf. *lineata*: several chemosensory setae, but not in a defined patch (scored 0). *Neato*: the palp is very similar to that of *Meedo* in proportions and ventral setae, but there is no dorsal chemosensory patch (scored 0). *Malenella*: the blunt setae mentioned in Ramírez (1995, 2003) are chemosensory.

84. Female palpal tarsus chemosensory patch configuration: 0. On dorsoapical surface (fig. 40C). 1. On apical truncation (fig. 40J, K, I). COMMENTS: *Lamponella*: large truncation, interpreted as a thickened palp, see character 82 (scored 0).

85. Palpal claw: 0. Present, well formed (figs. 37A, B, 39A). 1. Reduced to nubbin (figs. 35H, 37E, F). 2. Absent (fig. 37D). States are ordered, as in both Salticidae and Prodidominae there seems to be a sequence from a claw reduced to a nubbin, to absent. This character expresses the more drastic reductions in palpal claws. Platnick (2002) proposed the short palpal claws, shorter than the surrounding thick setae, as a synapomorphy of Ammoxenidae. The palpal claw of *Rastellus* seems well developed, and the apical setae are very long (fig. 40B). COMMENTS: *Malenella*, *Cheiramiona*, cf. Eutichuridae QLD: small claw, teeth reduced or absent (scored 0). Eutichuridae MAD: claw transverse (scored 0). *Meriola*: small, blunt. *Ammoxenus*: claw small but normal. *Prodidomus*: observed with compound microscope. *Neozimiris*: nubbin with one tooth (scored 1). *Aphantochilus*: distinguishable nubbin (scored 1).

86. Palpal claw teeth: 0. One to several teeth (figs. 38E, 39A). 1. No teeth (figs. 37C, 40G). COMMENTS: *Desis*: short teeth (scored 0). *Toxopsiella*, *Lauricius*: some in double row, presumedly abnormal (scored 0). *Brachyphaea*: from *B. simoni* syntype. *Otacilia*: small teeth (scored 0). *Drassinella*: contra Bosselaers and Jocqué (2000: char 157) (scored 0). *Teutamus*: only one very shallow tooth (scored 0). *Neozimiris*: one tooth, even if reduced claw (scored 0). Cf. Eutichuridae QLD: one tooth. *Heteropoda*: peculiarly curved claw (fig. 38E) (scored 0).

87. Palpal claw apex truncate: 0. Pointed (fig. 39A). 1. Truncate (figs. 34L, 39F). A truncate palpal claw is here found in *Lessertina* (Eutichuridae), *Paccius* and *Trachelas mexicanus* (Trachelidae), all with reduced leg spination, at least on legs I–II. The same palpal morphology appears in a group of species of *Philisca* (Anyphaenidae; Ramírez, 1993: fig. 4; 2003: char. 31, fig. 101A–E) with much reduced leg spination. This coincidence suggests a probable genetic correlation between leg spine reduction and truncate palpal claws. COMMENTS: *Meriola*: rounded (scored 01). *Paccius*: obliquely truncate (scored 1). *Mandaneta*: often broken (scored 0). *Agroeca*:

very often broken (scored 0). *Holcolaetis*: rounded tip (fig. 37B) (scored 01).

Sternum and Pleural Area

The sternum may bear sclerotized prolongations toward the center of a coxa (precoxal triangle) or between coxae (intercoxal extensions). Sometimes these extensions are separated from the sternum by a membranous strip. The pleural area between coxae and carapace bears small horizontal sclerites, the pleural bars, usually one above each coxa (fig. 41B).

88. Sternum length vs width: 0. Longer than wide (fig. 42A). 1. Wider than long (fig. 43H). Scored (01) when length and width are about the same. Comments: *Doliomalus,* Eutichuridae MAD, *Paravulsor*, *Titanebo*, *Eusparassus*: about the same (scored 01). *Odo bruchi*: slightly longer (scored 0).

89. Sternum shape: 0. Shield shaped, about straight anteriorly, convex sides, and pointed posteriorly (fig. 42A). 1. Oval, both anterior and posterior margins convex (fig. 43F). 2. Very elongate, as in *Aphantochilus* (fig. 43A). This is a simplified character to recover some of the information in the widely variable sternum shapes. Comments: *Lampona*: anteriorly constricted between coxae I (scored 0). *Austrachelas*: embracing the base of labium (scored 0). *Ammoxenus*, *Anyphops*: oval in general, but posteriorly prolonged (fig. 43E) (scored 01). *Vectius*: about oval, but posteriorly concave (fig. 43G) (scored 1). *Holcolaetis*, *Lyssomanes*, *Plexippus*, *Lyssomanes*: intermediate (scored 01).

90. Sternum anterior lateral surface: 0. Smooth or convex (fig. 42G). 1. Excavated (fig. 42C). These excavations are characteristic of some Corinninae, but none in this dataset (Bonaldo, 2000). Comments: *Sesieutes*, *Pronophaea*: not excavated but deeply rebordered (figs. 42A, 43C) (scored 0).

91. Sternum posterior end profile: 0. Convex or straight (fig. 42A). 1. Notched (fig. 42G). Comments: *Eriauchenius*: just slightly concave, articulating with ventral sclerite of pedicel (scored 0). *Oxyopes*: well extended between coxae (scored 0). *Vectius*: posteriorly concave but very widely so (fig. 43G) (scored -).

92. Sternum texture: 0. Smooth (fig. 43C). 1. Rugose, setal bases raised (fig. 42A, H, I). 2. Holes with central seta. The sternum has round depressions, similarly as in *Orthobula*, but with a central seta, present in *Lamponella* (Platnick, 2000: fig. 35). Comments: *Corinna*: raised round setae bases (scored 1). *Trachelas mexicanus*: slightly rugose (scored 01). *Orthobula*, *Teutamus*: holes with central pore, already scored for the carapace (see char. 5) (scored 0). Trachelidae ARG: smooth (scored 0). *Oedignatha*: fine polygonal mesh (scored 0).

93. Sternal sigilla: 0. None. Sometimes the sternal slit sensilla are very conspicuous, but these are not sigilla (fig. 43D). 1. On sternal margin between coxae III–IV (figs. 29B, 41D, E). This state is characteristic of Filistatidae. 2. On sternal margin at base of labium (fig. 18A) (Marples, 1968). Comments: *Hypochilus*: Marples (1968), from cleared specimens. He reported three sternal pairs in *Ectatosticta*, but only the labial one in *Hypochilus* (scored 2). *Filistata*: whitish marks, like invaginations of the sternal margin, with sigillalike surface, opposing III and IV (scored 1). *Castianeira*, *Brachyphaea*, *Paccius*, *Procopius*, *Mandaneta*, *Phrurotimpus* (fig. 43D), *Oedignatha*, *Systaria*: series of large slit sensilla opposing spaces between coxae, also common in other terminals (scored 0).

94. Fusion of sternum with pleural bars: 0. Free (fig. 41B). 1. Fused (fig. 41C). "Pleural bars are narrow, horizontal sclerites between coxae and carapace ("pièces épimériennes" of Simon 1892: 11)" (Bosselaers and Jocqué, 2002: 247). This character was used by Platnick (2002: char. 4) and Bosselaers and Jocqué (2002: char. 70). Fusion occurs scattered in Lamponidae, here present only in *Oedignatha*, where the epimeric sclerites are fused to the carapace as well (fig. 41C). Comments: *Pseudocorinna*, *Jacaena*, *Teutamus*: epimeric sclerites separated from sternum by thin membranous strips (fig. 43B) (scored 0).

95. Precoxal triangles in female: 0. Absent (fig. 42D). 1. Fused to sternum (figs. 29G, 41A, 42E). 2. Separate from sternum by a membranous strip. States are ordered; the few cases of separated precoxal triangles are derived from taxa with fused ones. "Precoxal triangles are small triangular sclerites sur-

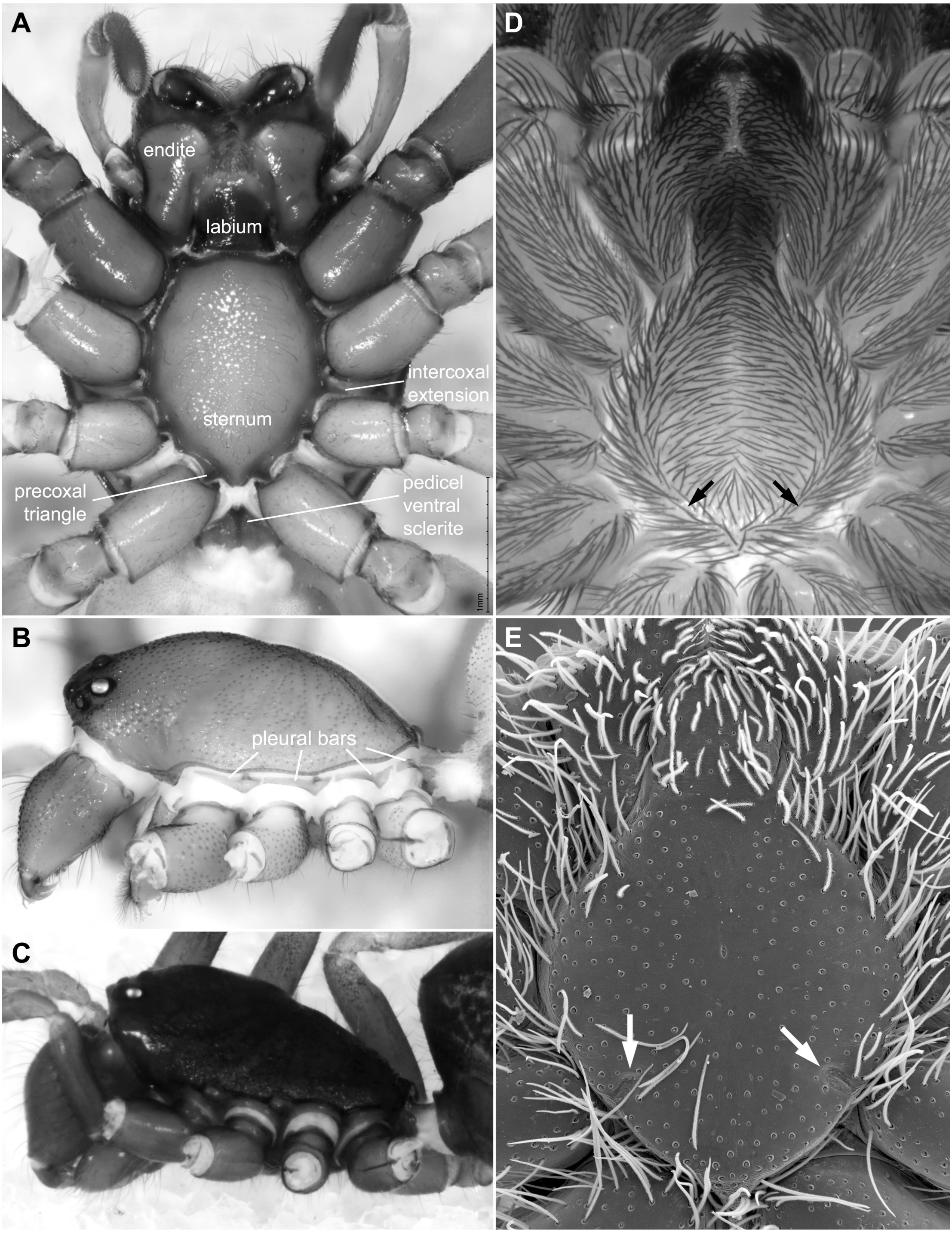

A
endite
labium
intercoxal extension
sternum
precoxal triangle
pedicel ventral sclerite
1mm
B
pleural bars
C
D
E

Fig. 41. Structures of sternum and pleural area, female. **A.** *Trachelas mexicanus* (Trachelidae). **B.** *Pronophaea proxima* (Corinnidae). **C.** *Oedignatha* sp. (Liocranidae). **D.** *Filistata insidiatrix* (Filistatidae), arrows to sigilla. **E.** *Pikelinia tambilloi* (Filistatidae), arrows to sigilla.

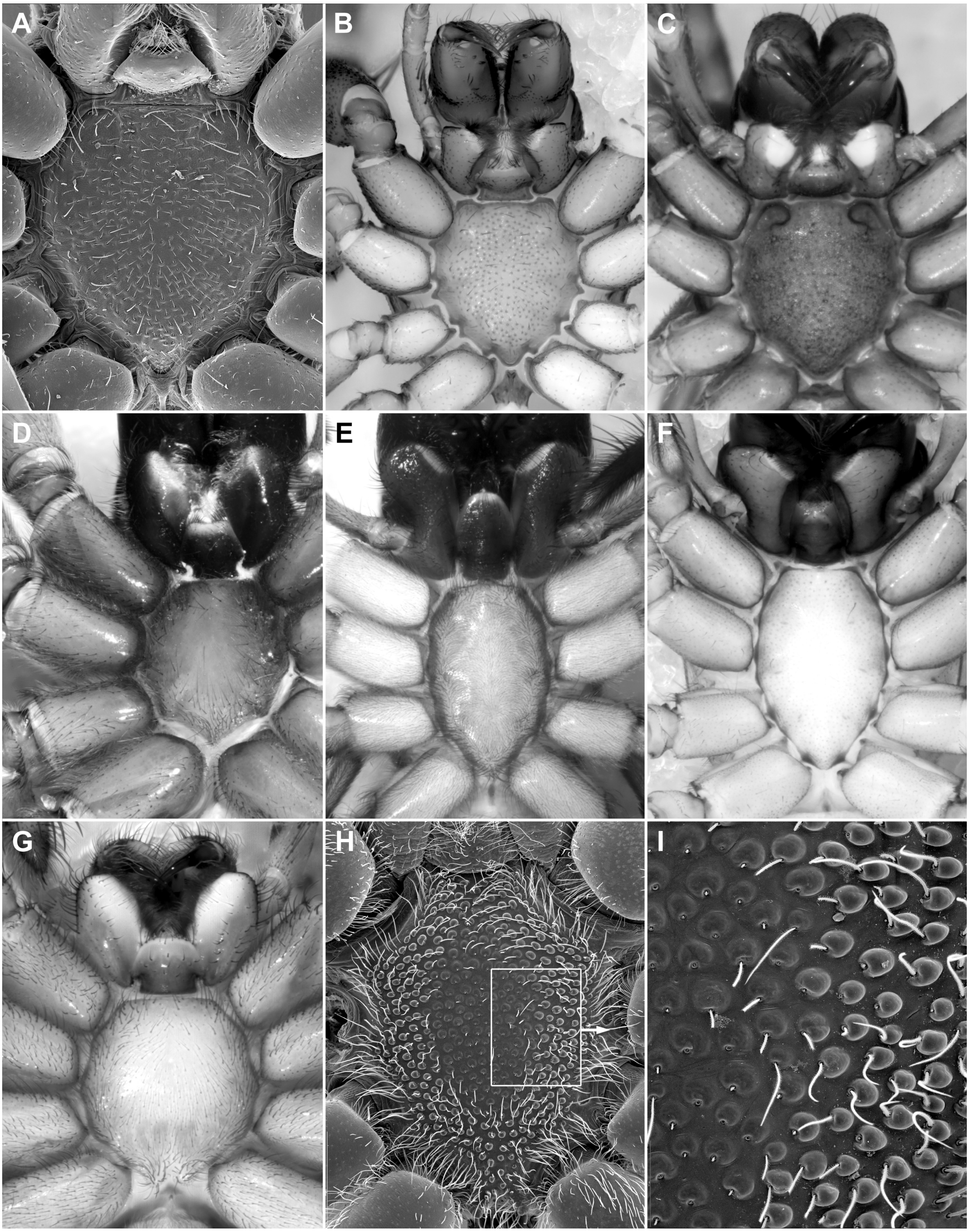


Fig. 42. Sternum of female. **A.** *Pronophaea proxima* (Corinnidae). **B.** Same, cephalothorax ventral. **C.** *Stethorrhagus* sp. (Corinnidae). **D.** *Miturga lineata* (Miturgidae). **E.** *Elaver* sp. (Clubionidae). **F.** *Amaurobioides pallida* (Anyphaenidae). **G.** *Selenops debilis* (Selenopidae). **H.** *Palpimanus transvaalicus* (Palpimanidae) female, inset in I. **I.** Same, sternum cuticle.

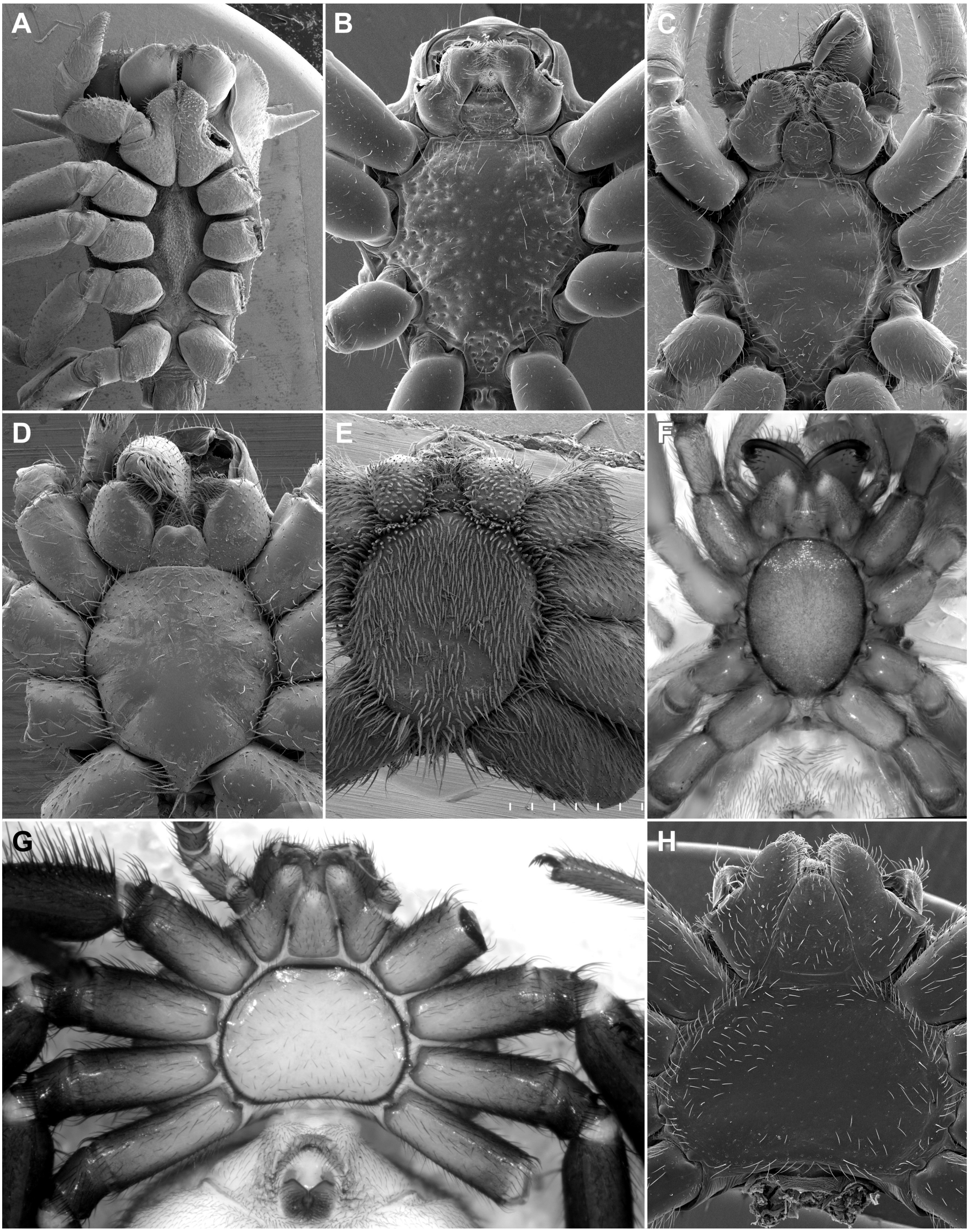


Fig. 43. Cephalothorax ventral, female. **A.** *Aphantochilus rogersi* (Thomisidae). **B.** *Teutamus* sp. (Liocranidae). **C.** *Sesieutes* sp. (Liocranidae). **D.** *Phrurotimpus alarius* (Phrurolithidae). **E.** *Ammoxenus coccineus* (Ammoxenidae). **F.** *Prodidomus redikorzevi* (Prodidomidae). **G.** *Vectius niger* (Gnaphosidae). **H.** Same, detail.

rounding the sternum, their tips facing the bases of the coxae (Penniman, 1985: 16). They may be free, or fused with the sternum" (Bosselaers and Jocqué, 2002: 247, chars. 65, 66; Silva Davila, 2003: char. 76, state 1). COMMENTS: *Filistata*, *Ctenus*: there are precoxal longitudinal bars before coxa I (scored 0). *Oxyopes*: with sternal extensions (scored 0). *Trachelas minor*: very faint projections (scored 0). *Paradiestus*: only weakly sclerotized (scored 01). *Agroeca*: very faint sclerotizations (scored 01). *Anagraphis*: some wide extensions might be homologous (scored 0). *Camillina*, *Austrachelas*: covered by membrane (scored 1). *Eilica*: apparently detached, may be an illusion from being covered by membrane (scored 2). *Micaria*: dark unsclerotized markings (scored 0). Cf. Eutichuridae QLD: short (scored 1). *Lessertina*: coxae too close to sternum (scored 12). *Macerio*: only on leg I (scored 2). *Boliscus*: absent in subadult female (scored 0). *Xysticus*: on legs III and IV (scored 2).

96. Detached intercoxal sternum extensions: 0. Absent (fig. 42F) or fused to sternum (fig. 42B). 1. Present (fig. 42E). COMMENTS: *Storenomorpha*: prolonged into pleural bars (scored 0). *Clubiona, Elaver*: between endite and I, and I and II (scored 1). *Falconina*: fused, covered by membrane (scored 0). *Procopius*: hard to tell if fused or not (scored 01). *Olbus*: fused, between I and II (scored 0). Cf. *Medmassa* THA, cf. Liocranidae LIB, *Teutamus*, *Lamponella*, *Austrachelas*: fused (scored 0). *Anyphaena*: before coxa I (scored 1). *Syspira*: small, internal, between I–II and II–III (scored 1). *Stephanopoides*: between I and II (scored 1).

LEGS

The four legs have the same number of articles and articular condyles (asterisks, fig. 44B). The generalities of leg joint articulations are summarized after Parry (1957) and Hill (1977). The rigid cuticular surfaces of legs and other body parts may have a uniformly or gradually varying scultpured surface (fig. 95K), or be divided in discrete cells (fig. 44G), as is typical of some araneoids. Discrete cells may have the distal margin elevated on top of the next cell, reminiscent of a slate tiling. In araneoids, other cuticular structures such as setal sockets, tarsal organ, or pore rims are often placed on individual cells by themselves. The abdominal cuticle is differently structured, is extensible to accommodate the ingesta, and has an accordionlike texture (fig. 102E).

COXA: The ventral basal corners of each coxa have fields of propriosensory setae ("hair plates"), which are deflected by the folding of the pleural membrane (fig. 44F). Most spiders have a breakage zone between coxa and trochanter, where leg autospasy occurs. For this reason, virtually all leg muscles between coxa and trochanter attach to small intermediate sclerites forming a ring (fig. 44E). Upon leg autospasy, the cleavage occurs across the sclerites, thus leaving the coxal muscles intact. The retrolateral surface of the coxa I, sometimes also II and III, may have an unsclerotized, often elevated patch, the retrocoxal hymen (fig. 45D). The coxa-trochanter joint has one prolateral condyle, and the movement is free in all directions.

TROCHANTER: The trochanter may have a ventral distal indentation, the trochanteral notch (fig. 44C). The trochanter-femur joint has two condyles, one at each side, allowing movement in the vertical plane.

FEMUR: The femur-patella joint has two dorsal-lateral condyles making a dorsal hinge, allowing movement in the vertical plane.

PATELLA: The retrolateral distal margin of the patella is indented in an unsclerotized area, leading to one or two closely grouped lyriform organs (figs. 44D, 45E). The patella-tibia joint articulates on a single dorsal condyle, allowing horizontal movements only. The area of the retrolateral indentation is distorted by the movement, coincident with the placement of the lyriform propriosensor organs. The patella-tibia joint has a single dorsal medial condyle, allowing movements in the horizontal plane, capable of more retraction than protraction.

TIBIA: The tibia-metatarsus joint has two dorsal-lateral condyles making a dorsal hinge, allowing movement on the vertical plane.

METATARSUS: In cribellate spiders the metatarus IV has a patch of curved thick setae, usually arranged in one or more rows

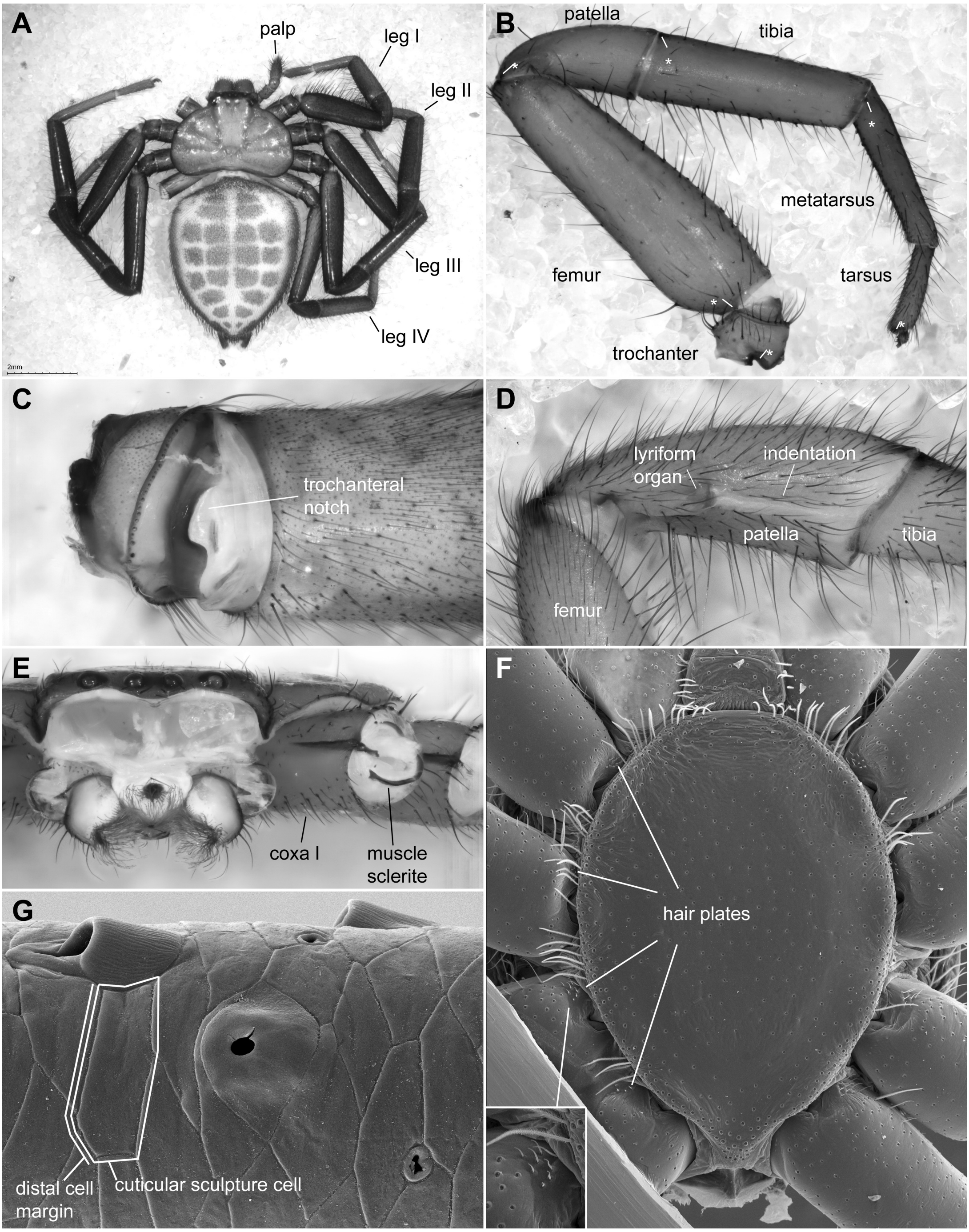

A
palp
leg I
leg II
leg III
leg IV
2mm
B
patella
tibia
metatarsus
femur
tarsus
trochanter
C
trochanteral notch
D
lyriform organ
indentation
patella
tibia
femur
E
coxa I
muscle sclerite
F
hair plates
G
distal cell margin
cuticular sculpture cell

Fig. 44. Structures of legs, female. **A.** *Vectius niger* (Gnaphosidae), habitus dorsal. **B.** *Doliomalus cimicoides* (Trochanteriidae), left leg I, prolateral. **C.** *Heteropoda venatoria* (Sparassidae), left trochanter I, ventral. **D.** *Macerio flavus* (Eutichuridae), right patella I, retrolateral. **E.** *Doliomalus cimicoides* (Trochanteriidae), cephalothorax anterior. **F.** *Prodidomus redikorzevi* (Prodidomidae), sternum and coxae. **G.** *Mimetus hesperus* (Mimetidae), cuticle and tarsal organ IV.

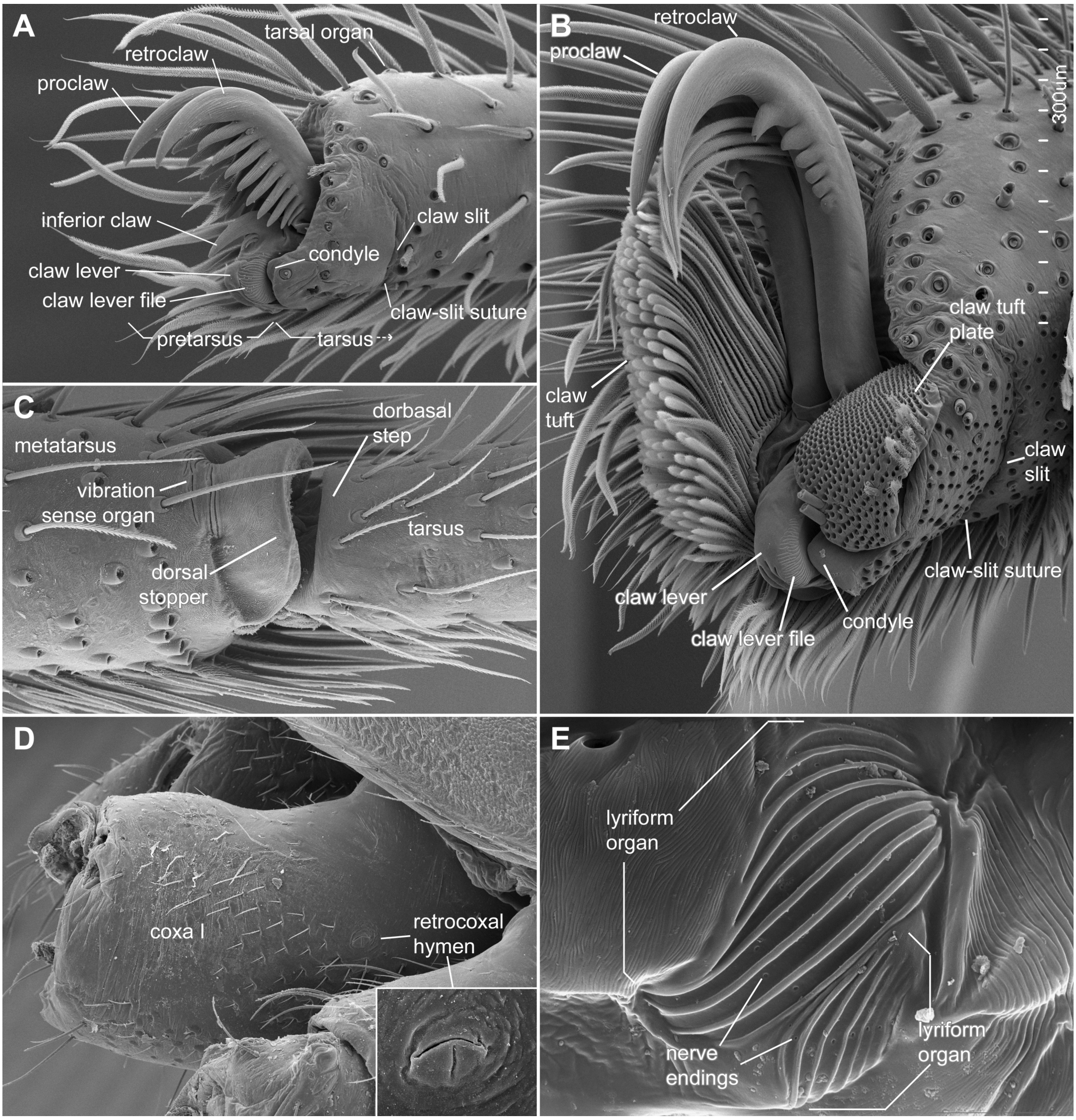

A
tarsal organ
retroclaw
proclaw
inferior claw
claw slit
condyle
claw lever
claw lever file
claw-slit suture
pretarsus
tarsus
B
retroclaw
proclaw
300um
claw tuft plate
claw tuft
claw slit
claw-slit suture
claw lever
condyle
claw lever file
C
dorbasal step
metatarsus
vibration sense organ
tarsus
dorsal stopper
D
coxa I
retrocoxal hymen
E
lyriform organ
nerve endings
lyriform organ

Fig. 45. Structures of legs, female. **A.** *Calacadia dentifera* (Amphinectidae), tarsal claws I, retrolateral. **B.** *Vulsor* sp. (Ctenidae), tarsal claws I, retrolateral-apical. **C.** *Meriola barrosi* (Trachelidae), tarsus-metatarsus IV joint, dorsal-prolateral **D.** *Falconina gracilis* (Corinnidae), coxa I, posterior-dorsal. **E.** Cf. *Patu* sp. (Symphytognathidae), lyriform organ on patella I, retrolateral.

along the dorsal-retrolateral margin (fig. 46C, D), but sometimes disposed on a less organized patch. The calamistrum is used for combing out silk from the cribellum. The calamistral setae usually have one or more rows of small teeth, which presumably card the cribellar fibrils (fig. 46E) (Foelix and Jung, 1978). Similarly as in most setae, calamistral setae were found to be innervated by three dentrites (Foelix and Jung, 1978). The metatarsus-tarsus joint has no condyle, and is free moving, but overflexion is limited by the dorsal metatarsal stopper. The metatarsal vibration sense organ (see Barth, 2002, and references therein) is a lyriform organ located at the dorsal end of the metatarsus, and is usually associated with a cuticular overhang,

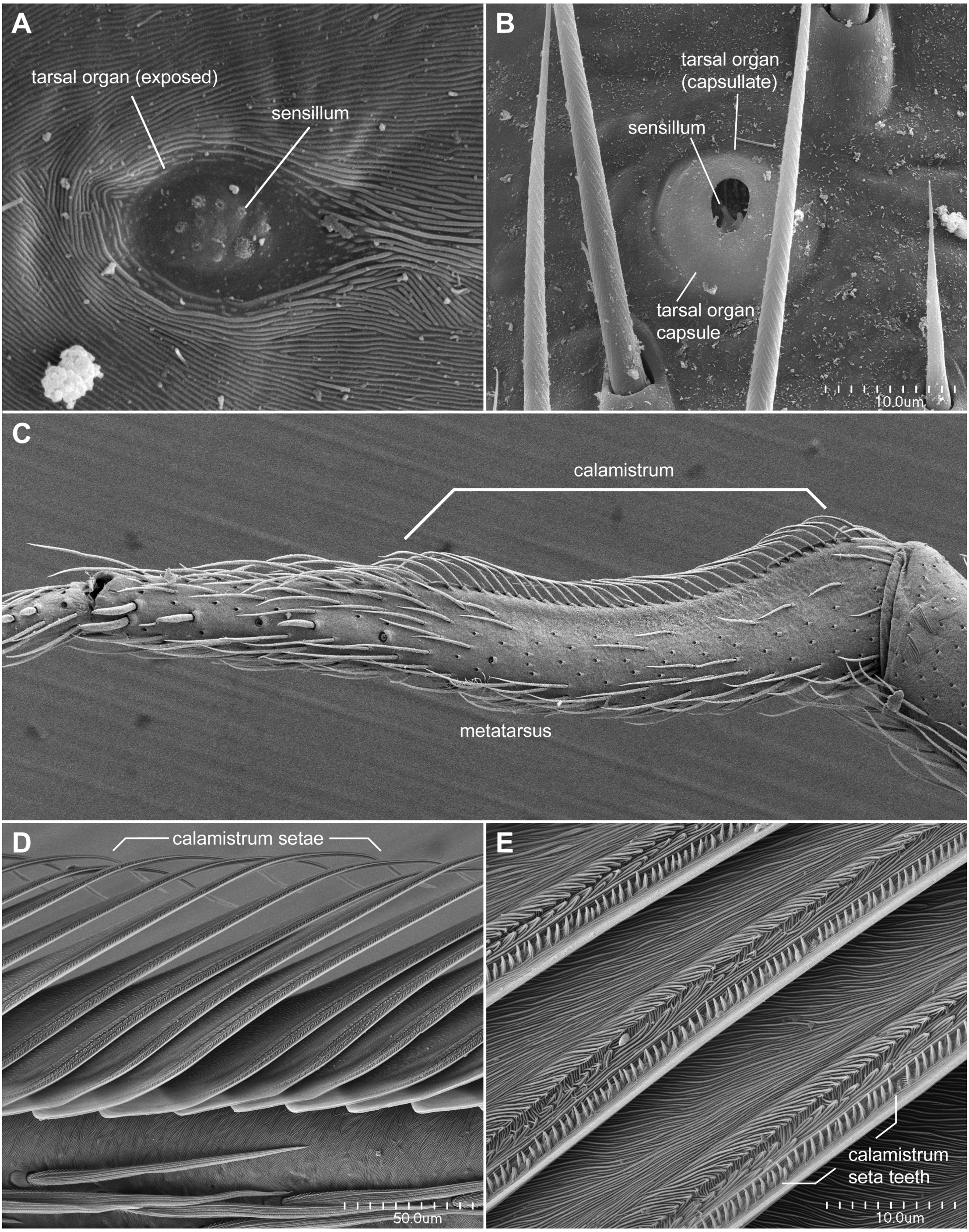

A
tarsal organ (exposed)
sensillum
B
tarsal organ (capsullate)
sensillum
tarsal organ capsule
10.0um
C
calamistrum
metatarsus
D
calamistrum setae
50.0um
E
calamistrum seta teeth
10.0um

Fig. 46. Structures of legs, female. **A.** *Thaida peculiaris* (Austrochilidae; image by Junxia Zhang), tarsal organ I. **B.** *Donuea* sp. ("Liocranidae"), tarsal organ IV. **C.** *Uloborus glomosus* (Uloboridae), metatarsus IV retrolateral. **D.** *Menneus* sp. from Tembe (Deinopidae), calamistrum setae, retrolateral. **E.** Same, detail.

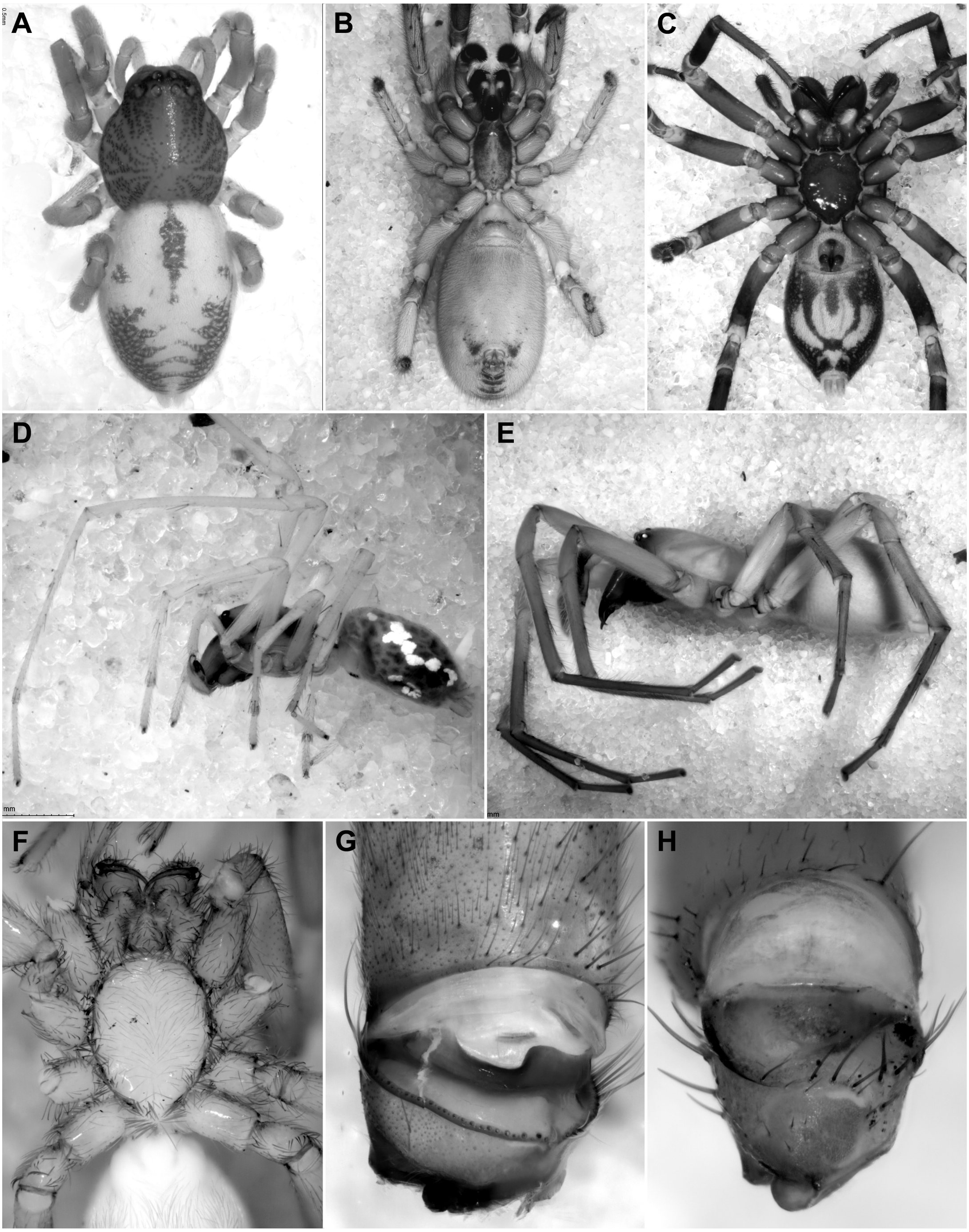


Fig. 47. Legs and trochanters. **A.** Trachelidae ARG female, dorsal. **B.** *Ariadna boesenbergi* (Segestriidae) female, ventral. **C.** *Desognaphosa yabbra* (Trochanteriidae) female, ventral. **D.** Eutichuridae MAD (Eutichuridae) male, lateral. **E.** *Eutichurus lizeri* (Eutichuridae) male, lateral. **F.** *Neozimiris pubescens* (Prodidomidae) male, cephalothorax ventral. **G.** *Heteropoda venatoria* (Sparassidae) female, left trochanter I, ventral. **H.** *Platyoides walteri* (Trochanteriidae) female, left trochanter I, ventral.

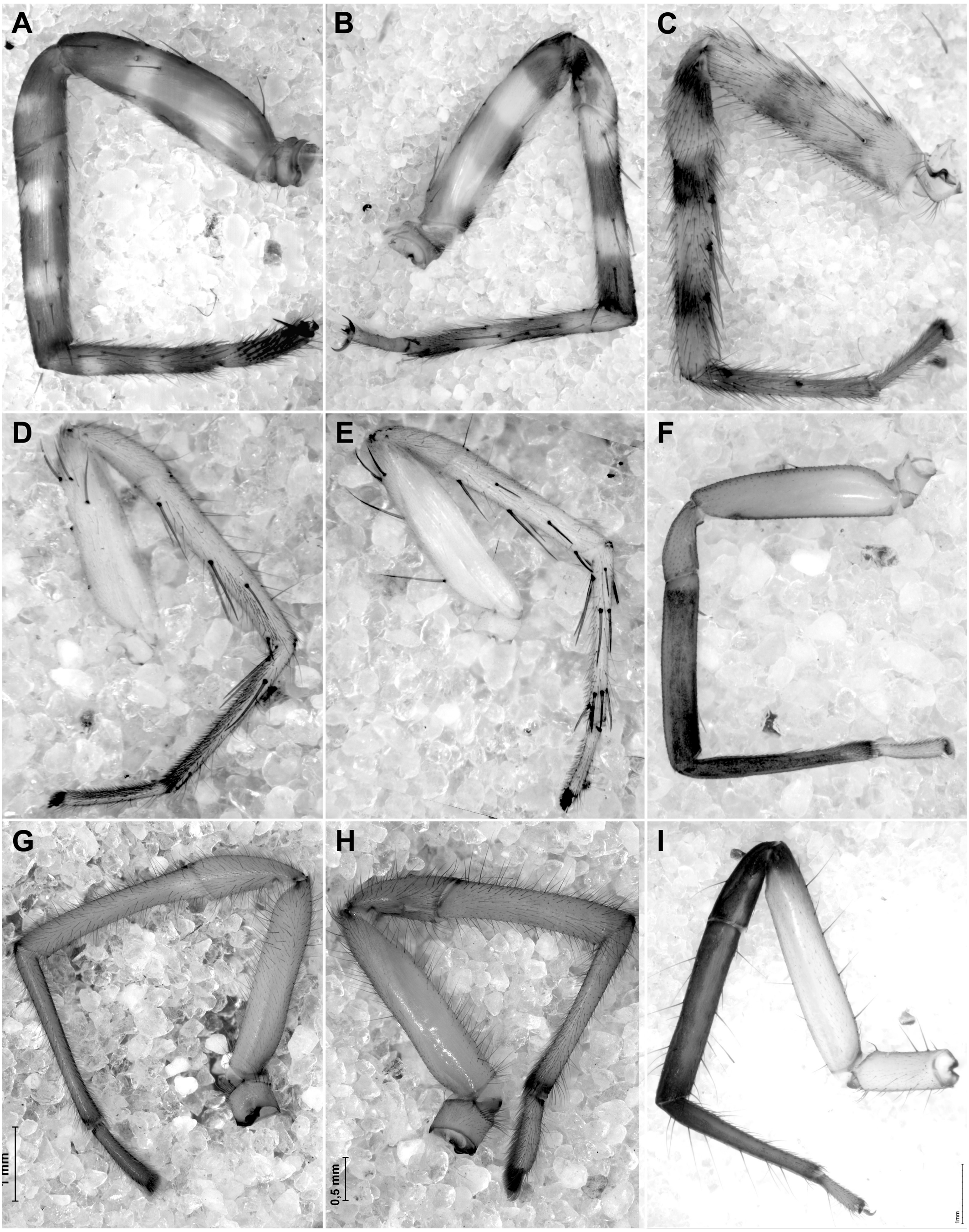


Fig. 48. Legs of female. **A.** *Tarlina woodwardi* (Gradungulidae), leg I, prolateral. **B.** *Tarlina woodwardi* (Gradungulidae), leg IV, retrolateral. **C.** *Selenops debilis* (Selenopidae), leg I, prolateral. **D.** *Gayenna americana* (Anyphaenidae), leg I, prolateral. **E.** *Gayenna americana* (Anyphaenidae), leg IV, retrolateral. **F.** *Pronophaea proxima* (Corinnidae), leg IV, retrolateral. **G.** *Macerio flavus* (Eutichuridae), leg I, prolateral. **H.** Same, leg IV, retrolateral. **I.** *Platyoides walteri* (Trochanteriidae), leg IV, retrolateral.

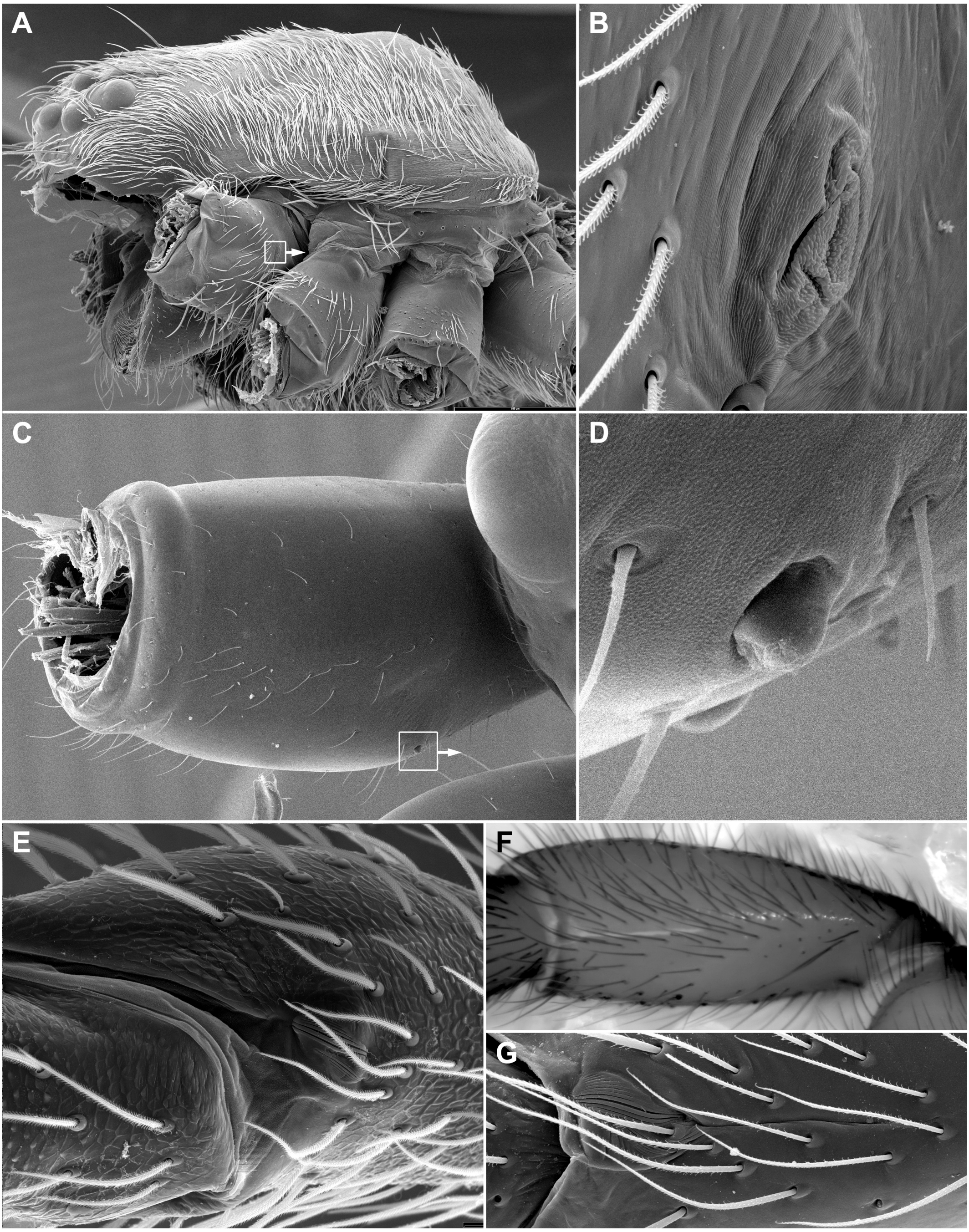


Fig. 49. Coxae and patellae, female. **A.** *Paravulsor* sp. (Miturgidae), cephalothorax lateral, inset on coxa I marking position of retrocoxal hymen. **B.** Same, detail of retrocoxal hymen. **C.** *Teutamus* sp. (Liocranidae), left coxa I, dorsal-posterior, inset on retrocoxal hymen. **D.** Same, detail of retrocoxal hymen. **E.** *Eriauchenius workmani* (Archaeidae), lyriform organ on left patella I, retrolateral. **F.** *Scelidocteus vuattouxi* (Palpimanidae), left patella I, retrolateral. **G.** Same, lyriform organ on left patella IV, retrolateral.

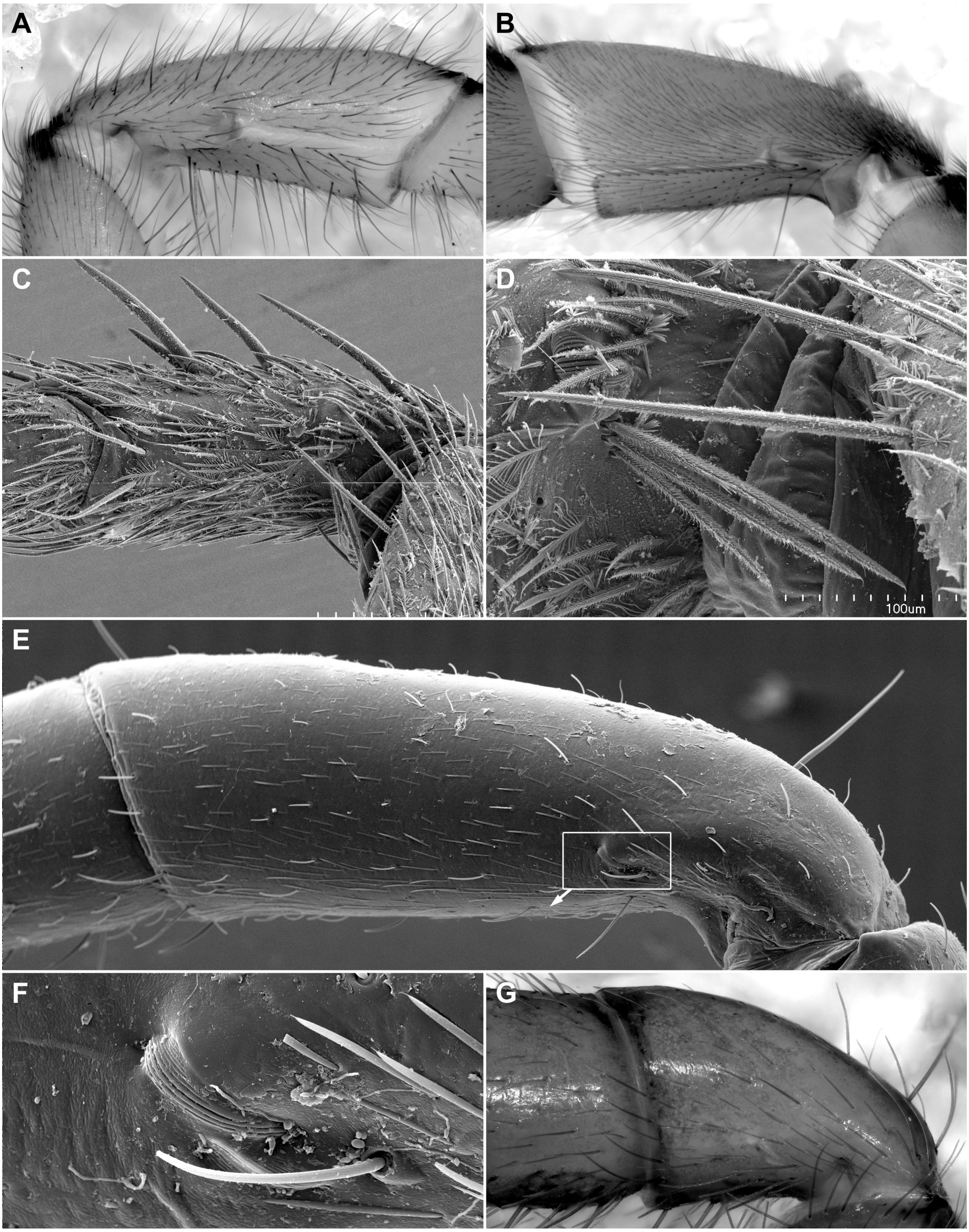


Fig. 50. Patellae of female, retrolateral. **A.** *Macerio flavus* (Eutichuridae). **B.** *Austrachelas pondoensis* (Gallieniellidae). **C.** *Ammoxenus coccineus* (Ammoxenidae), retrolateral-ventral. **D.** Same, detail of large setae ventral to lyriform organ. **E.** *Platyoides walteri* (Trochanteriidae), marked inset shown on F. **F.** Same, detail of lyriform organ. **G.** *Vectius niger* (Gnaphosidae).

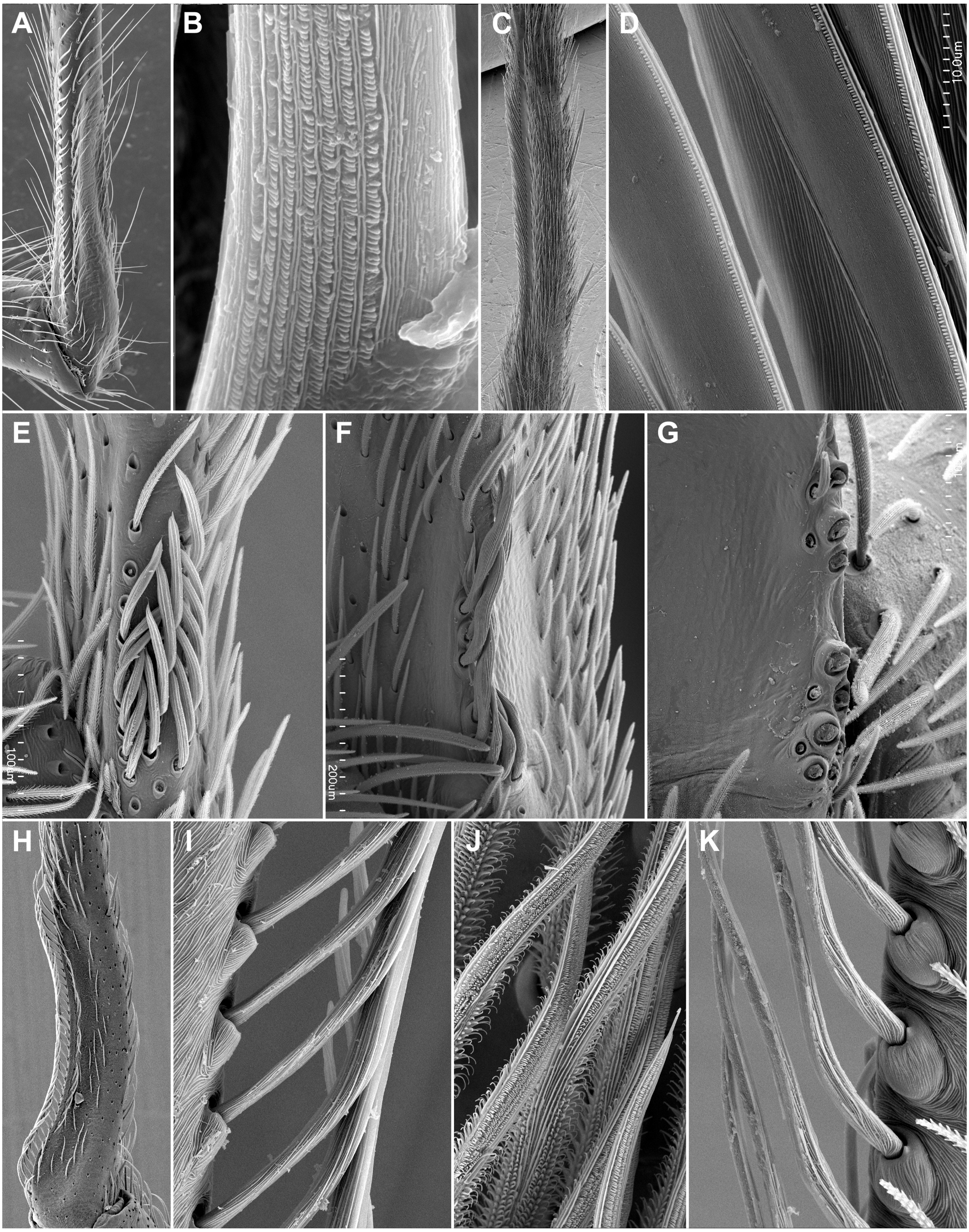


Fig. 51. Calamistrum, female. **A.** *Hypochilus pococki* (Hypochilidae). **B.** Same, detail of calamistrum seta. **C.** *Thaida peculiaris* (Austrochilidae). **D.** Same, detail of calamistrum setae. **E.** *Pritha nana* (Filistatidae). **F.** *Filistata insidiatrix* (Filistatidae), left. **G.** Same, right, calamistrum setae removed. **H.** *Uloborus glomosus* (Uloboridae). **I.** Same, detail of calamistrum setae. **J.** *Eresus* cf. *kollari* (Eresidae), detail of calamistrum setae. **K.** *Dictyna arundinacea* (Dictynidae), detail of calamistrum setae.

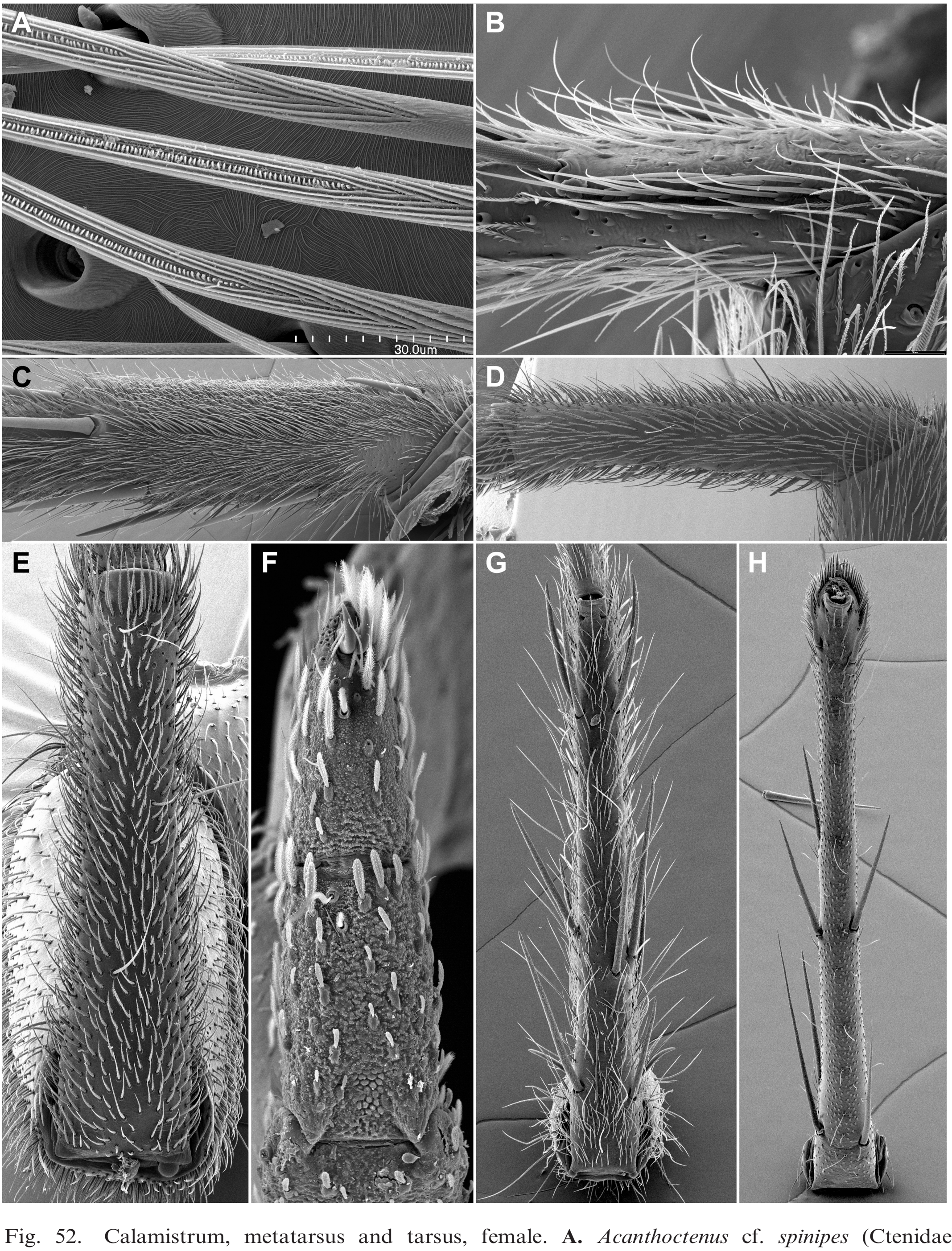


Fig. 52. Calamistrum, metatarsus and tarsus, female. **A.** *Acanthoctenus* cf. *spinipes* (Ctenidae), calamistrum setae. **B.** *Ciniflella* ARG (Tengellidae), left calamistrum. **C.** *Zorocrates gnaphosoides* (Zorocratidae), left calamistrum. **D.** *Cybaeodamus taim* (Zodariidae), left metatarsus I retrolateral. **E.** Same, dorsal. **F.** *Boliscus* cf. *tuberculatus* (Thomisidae), subadult female, left metatarsus and tarsus IV, dorsal. **G.** *Gayenna americana* (Anyphaenidae), left metatarsus IV, dorsal. **H.** *Donuea* sp. ("Liocranidae") right metatarsus IV, dorsal.

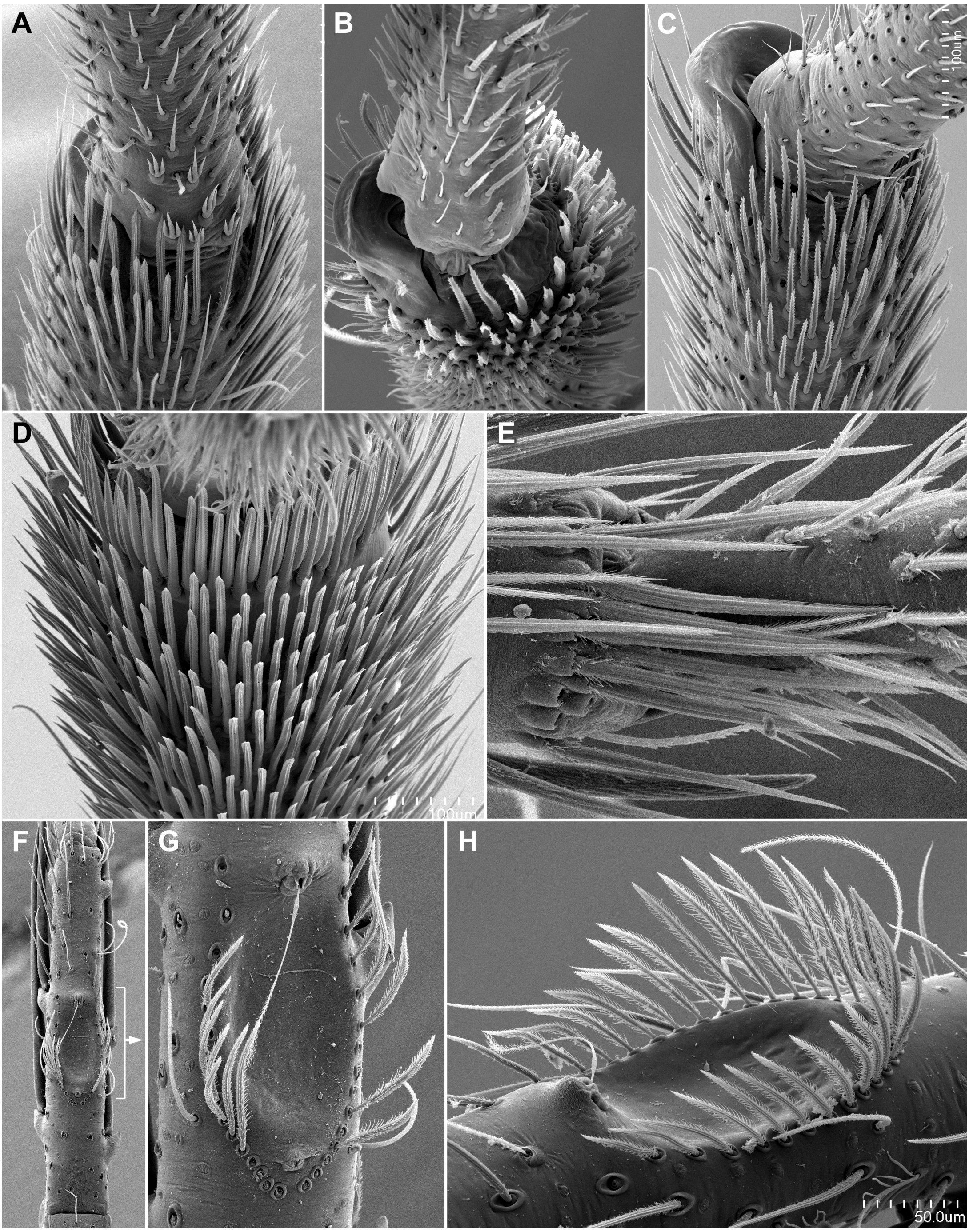


Fig. 53. Structures of metatarsi, female. A–E, ventral end of metatarsus IV. F–H, dorsum of metatarsus. **A.** *Pseudocorinna felix* (Corinnidae). **B.** *Jacaena* sp. (Liocranidae). **C.** *Sesieutes* sp. (Liocranidae). **D.** *Paccius* cf. *scharffi* (Trachelidae). **E.** *Camillina calel* (Gnaphosidae). **F.** *Hortipes merwei* ("Corinnidae"), metatarsus I, dorsal. **G.** Same, detail of metatarsal sensor. **H.** Same, sensor on metatarsus II.

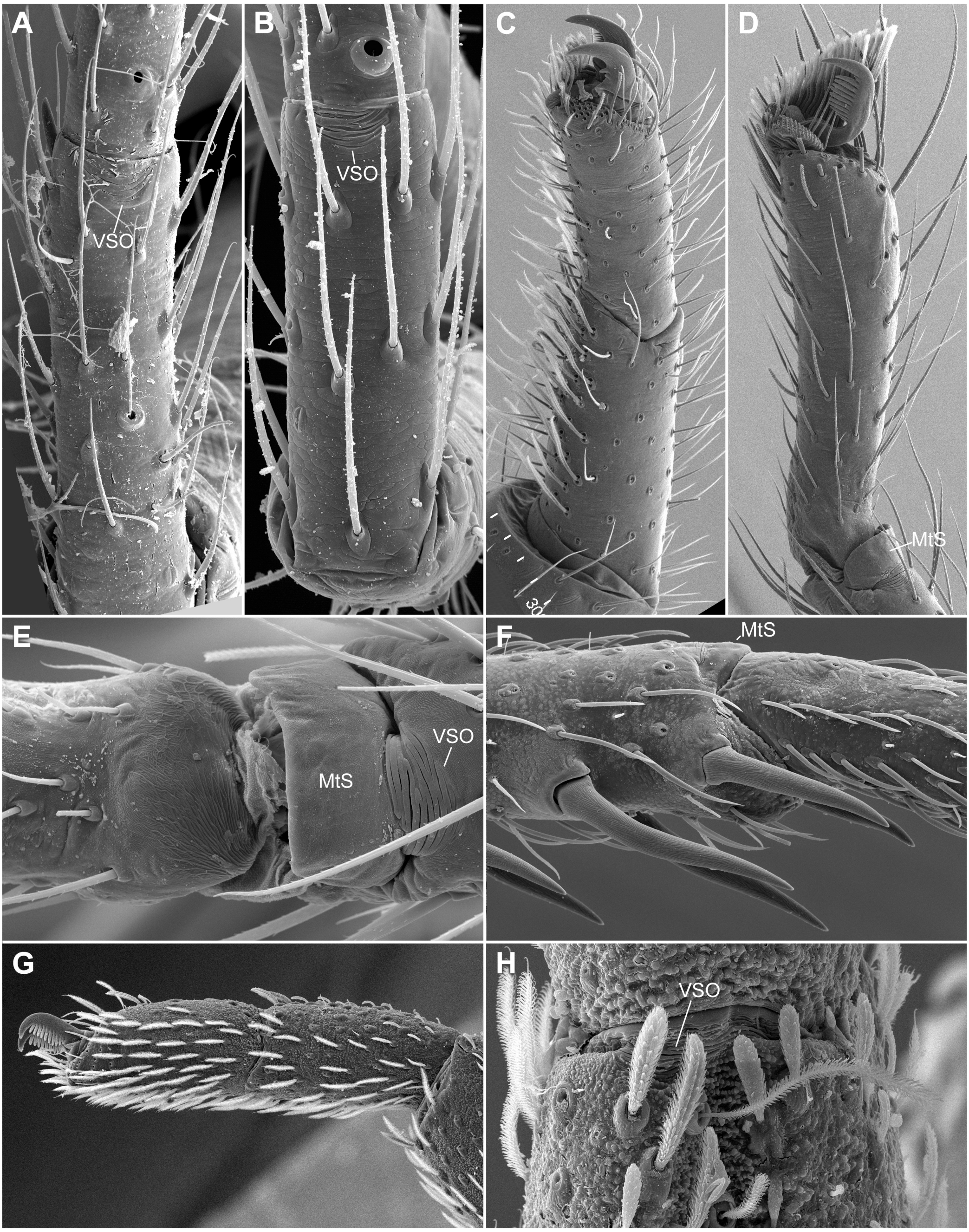


Fig. 54. Tarsus-metatarsus articulation, female. **A.** *Crassanapis chilensis* (Anapidae), right metatarsus I, dorsal (image by Lara Lopardo). **B.** *Textricella luteola* (Micropholcommatidae), right metatarsus IV, dorsal. **C.** *Hispo* sp. (Salticidae), left tarsus and metatarsus I, retrolateral. **D.** *Lyssomanes viridis* (Salticidae), left tarsus I, retrolateral. **E.** Same, detail of tarsus-metatarsus joint, dorsal. **F.** *Thomisus onustus* (Thomisidae), left tarsus-metatarsus joint I, prolateral. **G.** *Boliscus* cf. *tuberculatus* (Thomisidae), subadult female, left tarsus and metatarsus I, retrolateral. **H.** Same, detail of tarsus-metatarsus joint, dorsal.

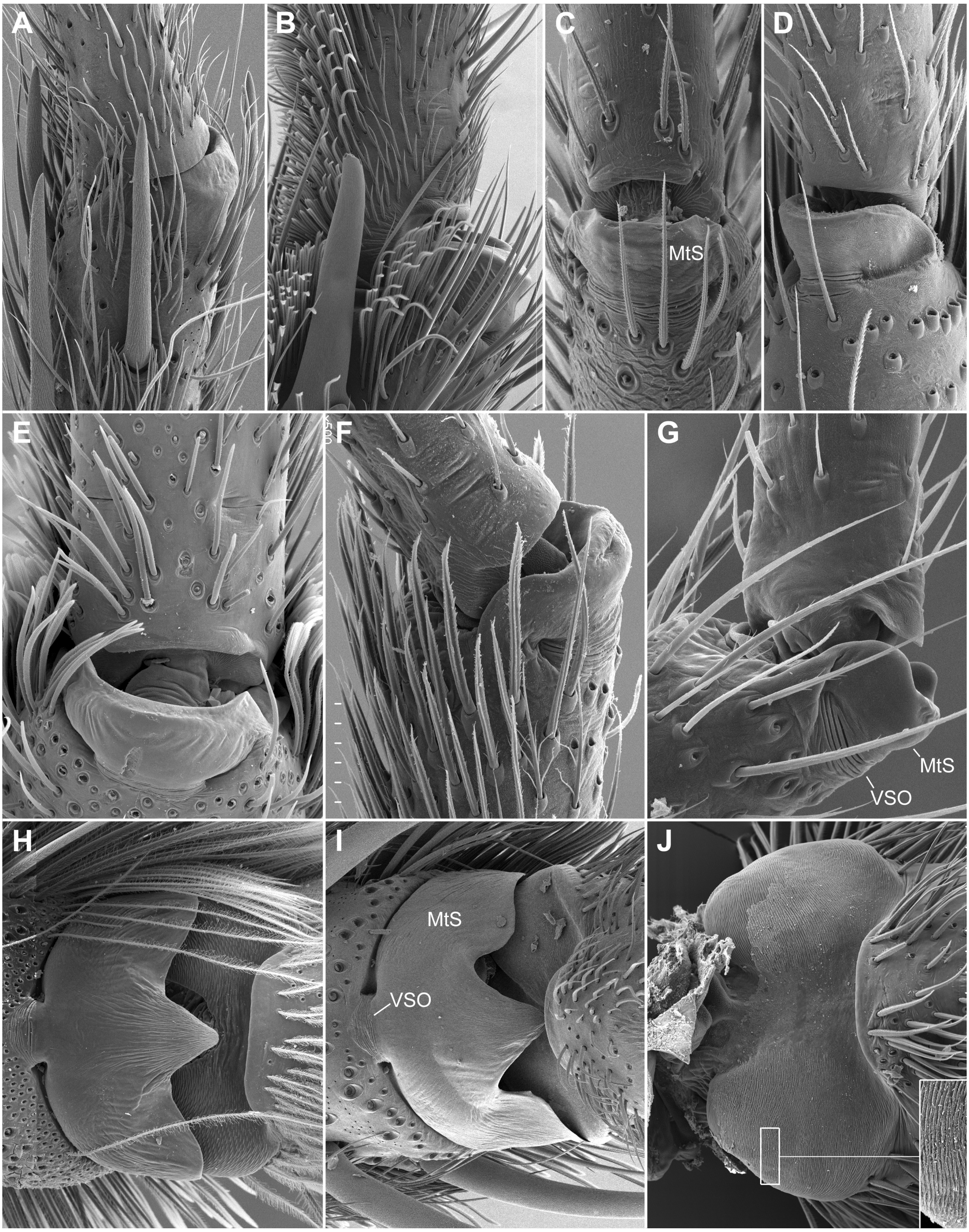


Fig. 55. Tarsus-metatarsus articulation, female. **A.** *Acanthoctenus* cf. *spinipes* (Ctenidae), left leg IV, retrolateral. **B.** *Ctenus* cf. *crulsi* (Ctenidae), left leg I, retrolateral. **C.** *Cithaeron delimbatus* (Cithaeronidae), right leg I, dorsal. **D.** *Meriola barrosi* (Trachelidae), left leg IV, dorsal. **E.** *Austrachelas pondoensis* (Gallieniellidae), left leg I, dorsal. **F.** *Otacilia* sp. (Phrurolithidae), left leg IV, retrolateral. **G.** *Teutamus* sp. (Liocranidae), left leg I, retrolateral. **H.** *Eusparassus* cf. *walckenaeri* (Sparassidae), **I.** *Heteropoda venatoria* (Sparassidae), left leg IV, dorsal. **J.** Same, base of left tarsus I, dorsal, inset to ridges.

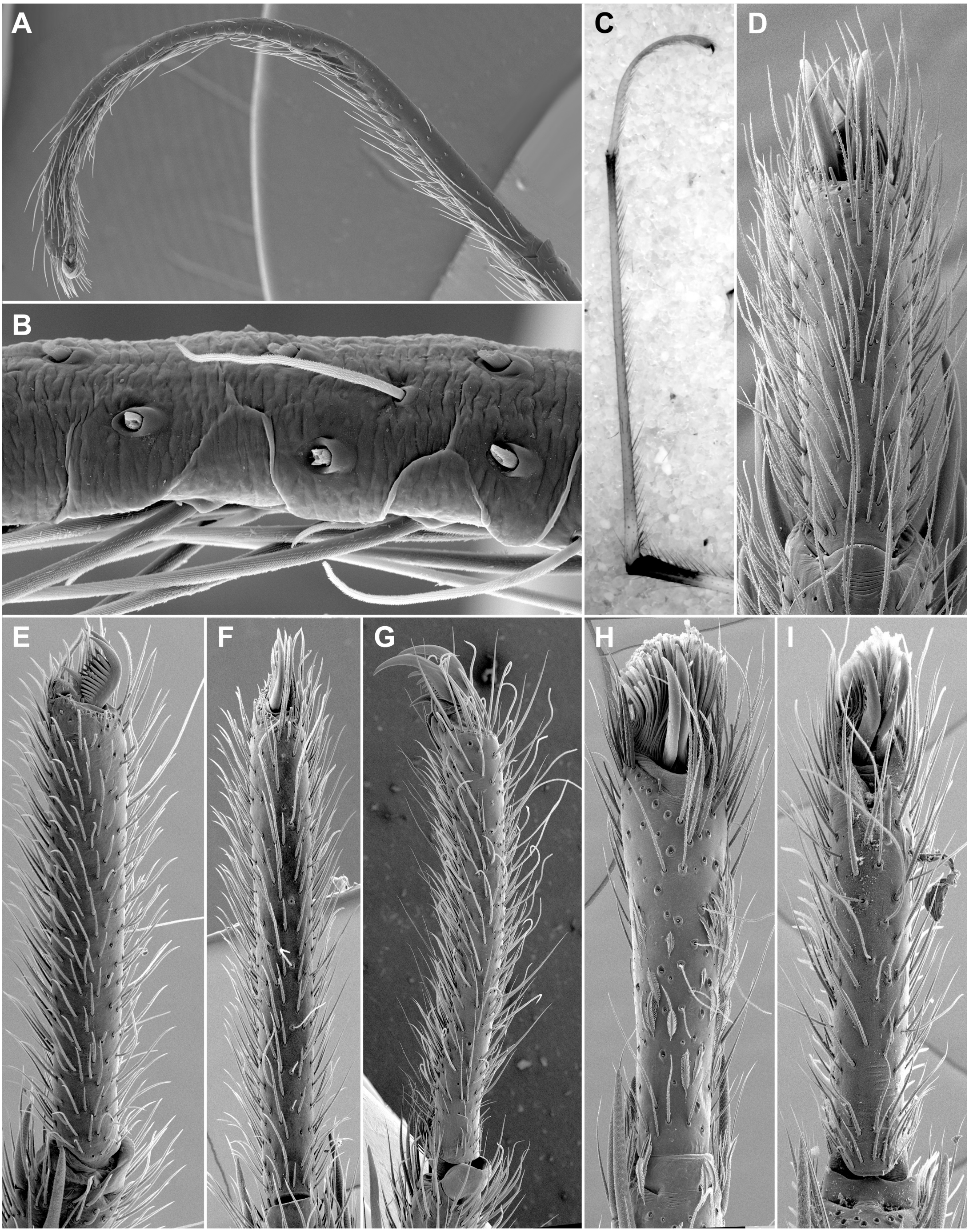


Fig. 56. Tarsi of female. **A.** *Hypochilus pococki* (Hypochilidae), left tarsus I, retrolateral. **B.** Same, detail. **C.** Same, left metatarsus and tarsus I, prolateral. **D.** *Ariadna boesenbergi* (Segestriidae), left tarsus I, dorsal. **E.** *Pimus napa* (Amaurobiidae), left tarsus I, retrolateral. **F.** Same, dorsal. **G.** *Cycloctenus nelsonensis* (Cycloctenidae), left tarsus I, retrolateral. **H.** *Holcolaetis* cf. *zuluensis* (Salticidae), left tarsus IV, dorsal. **I.** Sparianthinae VEN (Sparassidae), left tarsus IV, dorsal.

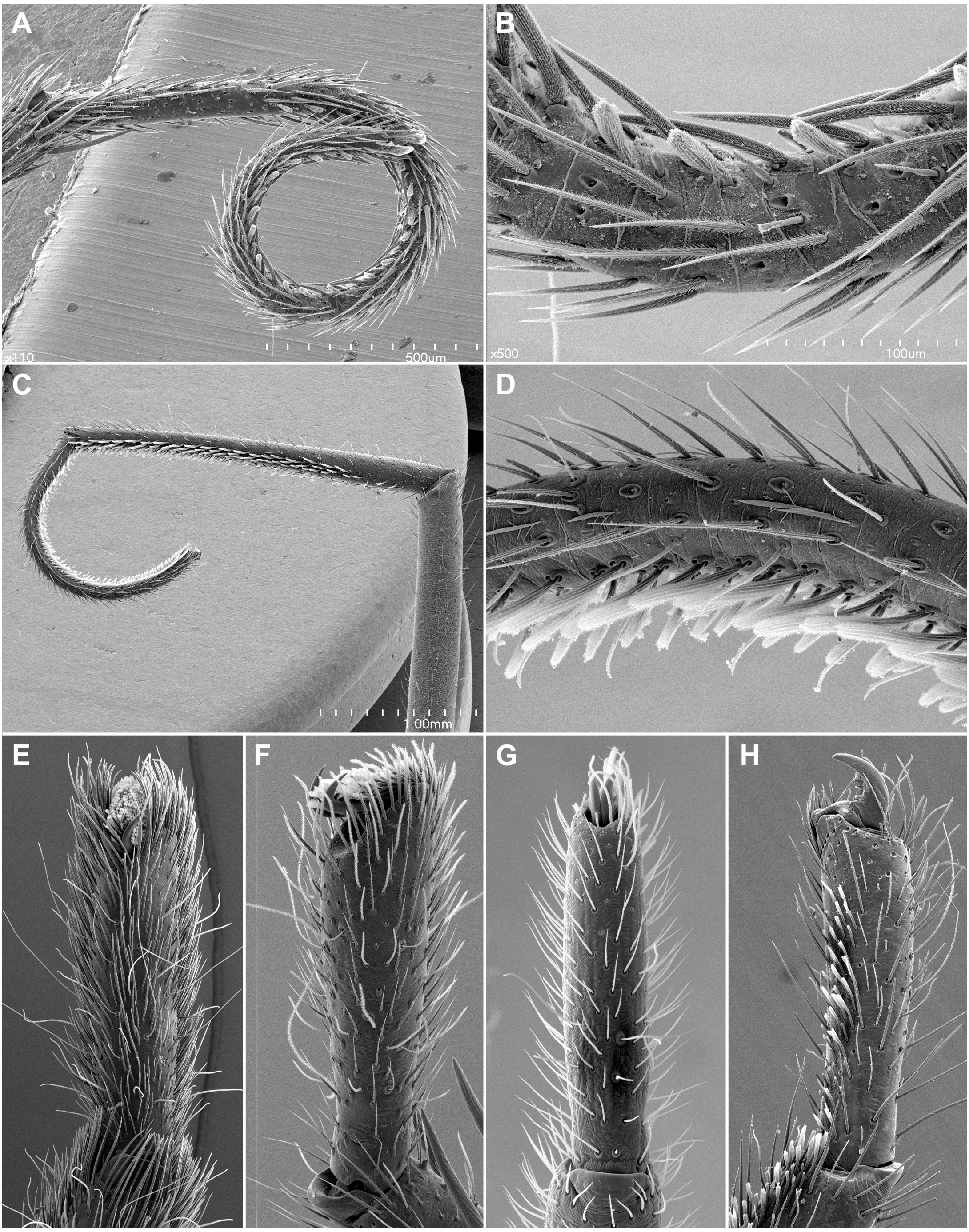


Fig. 57. Tarsi of female. **A.** *Ammoxenus coccineus* (Ammoxenidae), left tarsus, probably II, prolateral. **B.** Same, detail. **C.** *Cithaeron delimbatus* (Cithaeronidae), right tarsus I, retrolateral. **D.** Same, detail. **E.** *Brachyphaea* cf. *simoni* (Corinnidae), left tarsus IV, dorsal. **F.** *Pseudocorinna felix* (Corinnidae), left tarsus I, prolateral. **G.** *Lamponella brookfield* (Lamponidae), left tarsus I, dorsal. **H.** *Doliomalus cimicoides* (Trochanteriidae), left tarsus I, retrolateral.

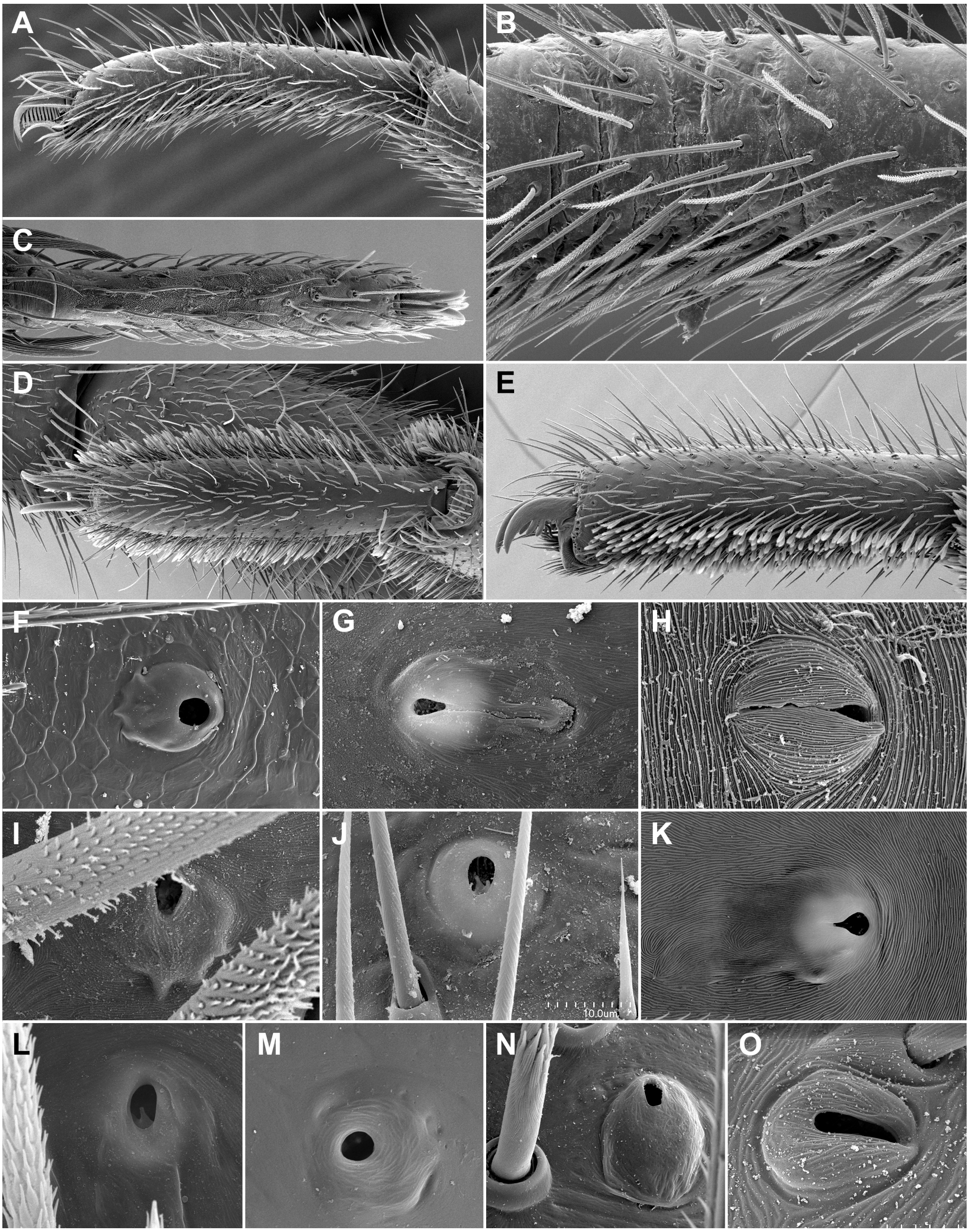


Fig. 58. Tarsi and tarsal organ of female. **A.** *Neato walli* (Gallieniellidae), left tarsus I, retrolateral. **B.** Same, detail. **C.** *Geraesta hirta*, left tarsus I, dorsal. **D.** *Gnaphosa taurica* (Gnaphosidae), left tarsus I, dorsal. **E.** Same, retrolateral. **F.** *Nicodamus mainae* (Nicodamidae), tarsal organ I. **G.** *Pimus napa* (Amaurobiidae), tarsal organ I. **H.** *Toxopsiella minuta* (Cycloctenidae), tarsal organ IV. **I.** *Zoropsis rufipes* (Zoropsidae), tarsal organ I. **J.** *Donuea* sp. ("Liocranidae"), tarsal organ IV. **K.** *Vulsor* sp. (Ctenidae), tarsal organ I. **L.** *Brachyphaea* cf. *simoni* (Corinnidae), tarsal organ IV. **M**. *Corinna bulbula* (Corinnidae), tarsal organ from palp. **N.** *Copa flavoplumosa* (Corinnidae), tarsal organ I. **O.** *Meriola barrosi* (Trachelidae), tarsal organ IV.

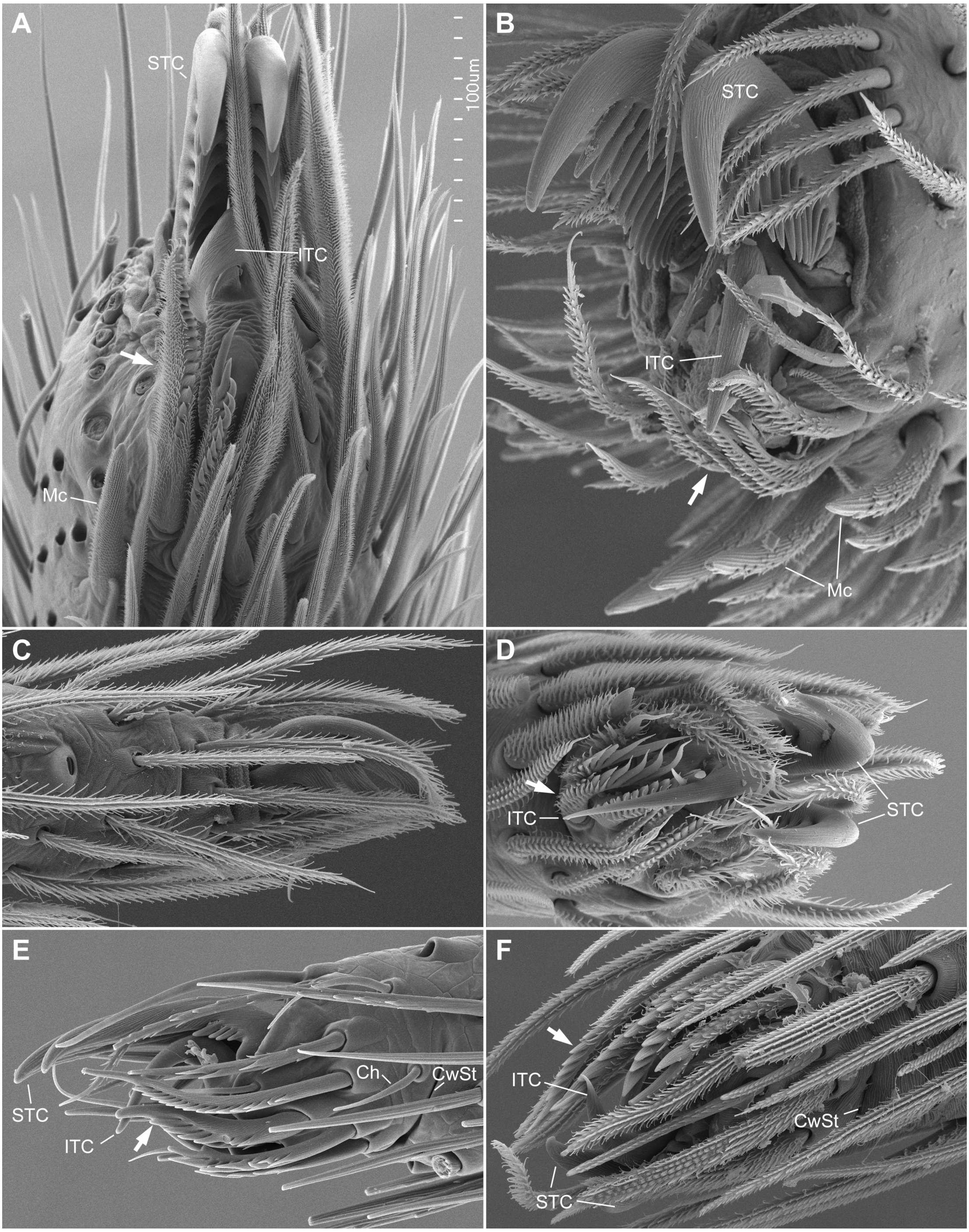

A
STC
100um
ITC
Mc
B
STC
ITC
Mc
C
D
ITC
STC
E
Ch
CwSt
STC
ITC
F
ITC
CwSt
STC

Fig. 59. Claws of female (arrows to serrate accessory claw setae). **A.** *Thaida peculiaris* (Austrochilidae), right IV, ventral. **B.** *Nicodamus mainae* (Nicodamidae), left IV, apical. **C.** *Eriauchenius workmani* (Archaeidae), left I, dorsal. **D.** Same, IV, ventral-apical **E.** *Mimetus hesperus* (Mimetidae), left IV, retrolateral. **F.** *Uloborus glomosus* (Uloboridae), left IV, ventral.

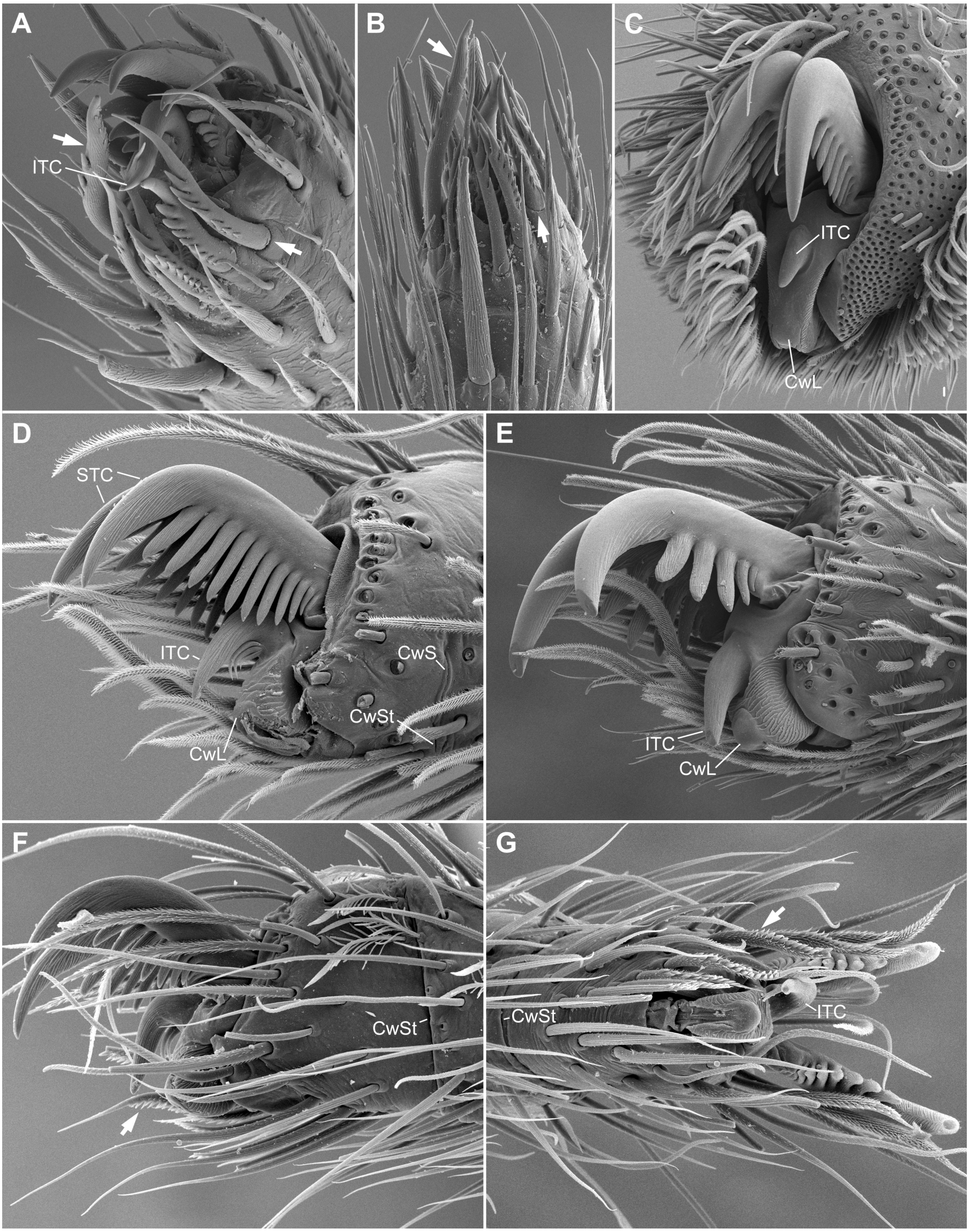

A
ITC
B
C
ITC
CwL
D
STC
ITC
CwS
CwSt
CwL
E
ITC
CwL
F
CwSt
G
CwSt
ITC

Fig. 60. Claws of female, left (arrows to serrate accessory claw setae). **A.** *Araneus diadematus* (Araneidae), IV, apical. **B.** Same, ventral. **C.** *Zorocrates gnaphosoides* (Zorocratidae), I, apical. **D.** *Pimus napa* (Amaurobiidae), I, retrolateral. **E.** *Trochosa ruricola* (Lycosidae), I, retrolateral. **F.** *Senoculus* sp. (Senoculidae), I, retrolateral. **G.** Same, ventral.

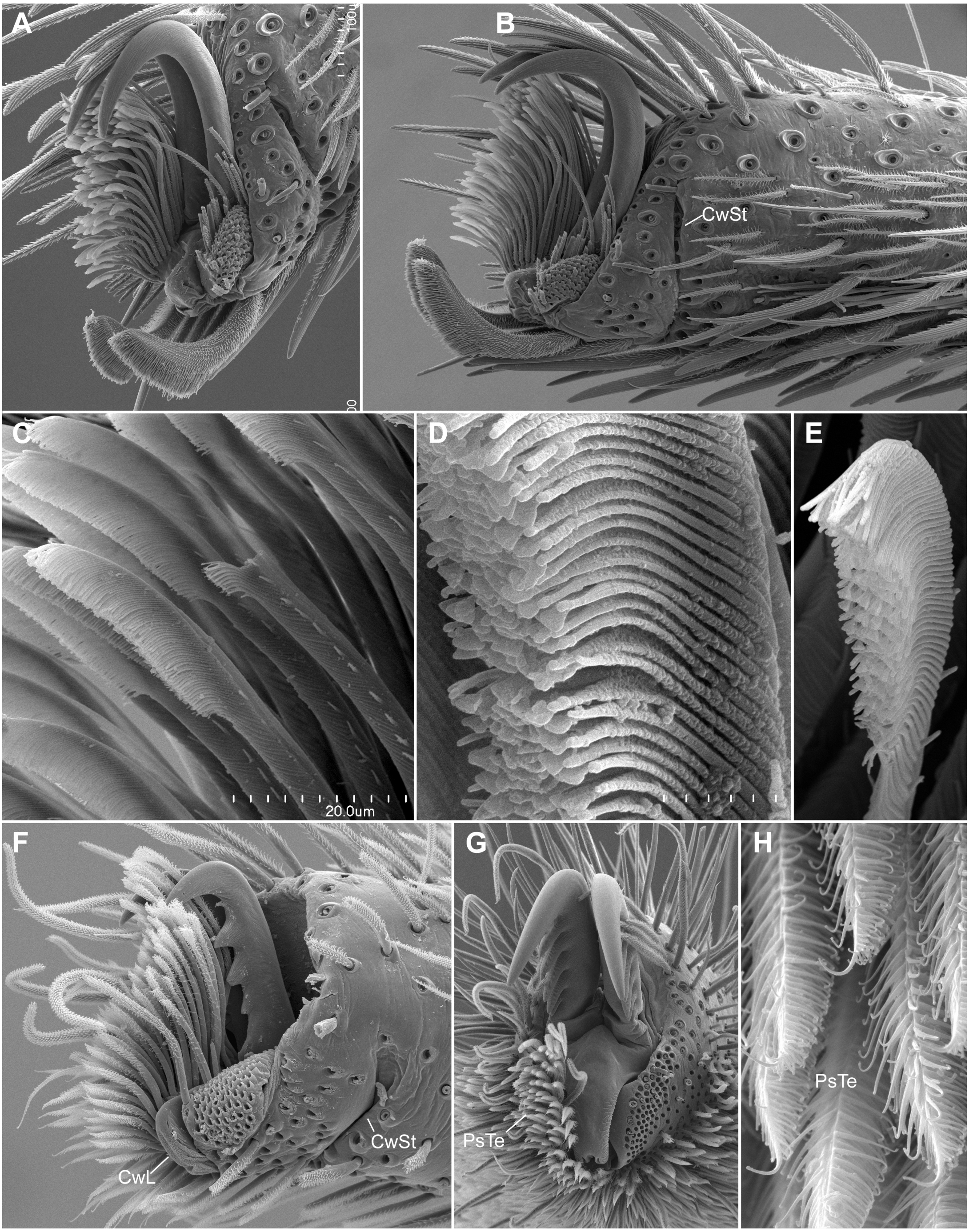


Fig. 61. Claws and claw tufts, female. **A.** *Homalonychus theologus* (Homalonychidae), left claws I, retrolateral-apical. **B.** Same, retrolateral. **C.** Same, detail of claw tuft. **D.** Same, detail of tenent barbs of claw tuft seta. **E.** Same, detail of claw tuft seta. **F.** *Pseudoctenus thaleri* (Zoropsidae), left claws I, retrolateral. **G.** *Uliodon* cf. *frenatus* (Zoropsidae), left claws I, apical. **H.** Same, detail of claw tuft setae IV.

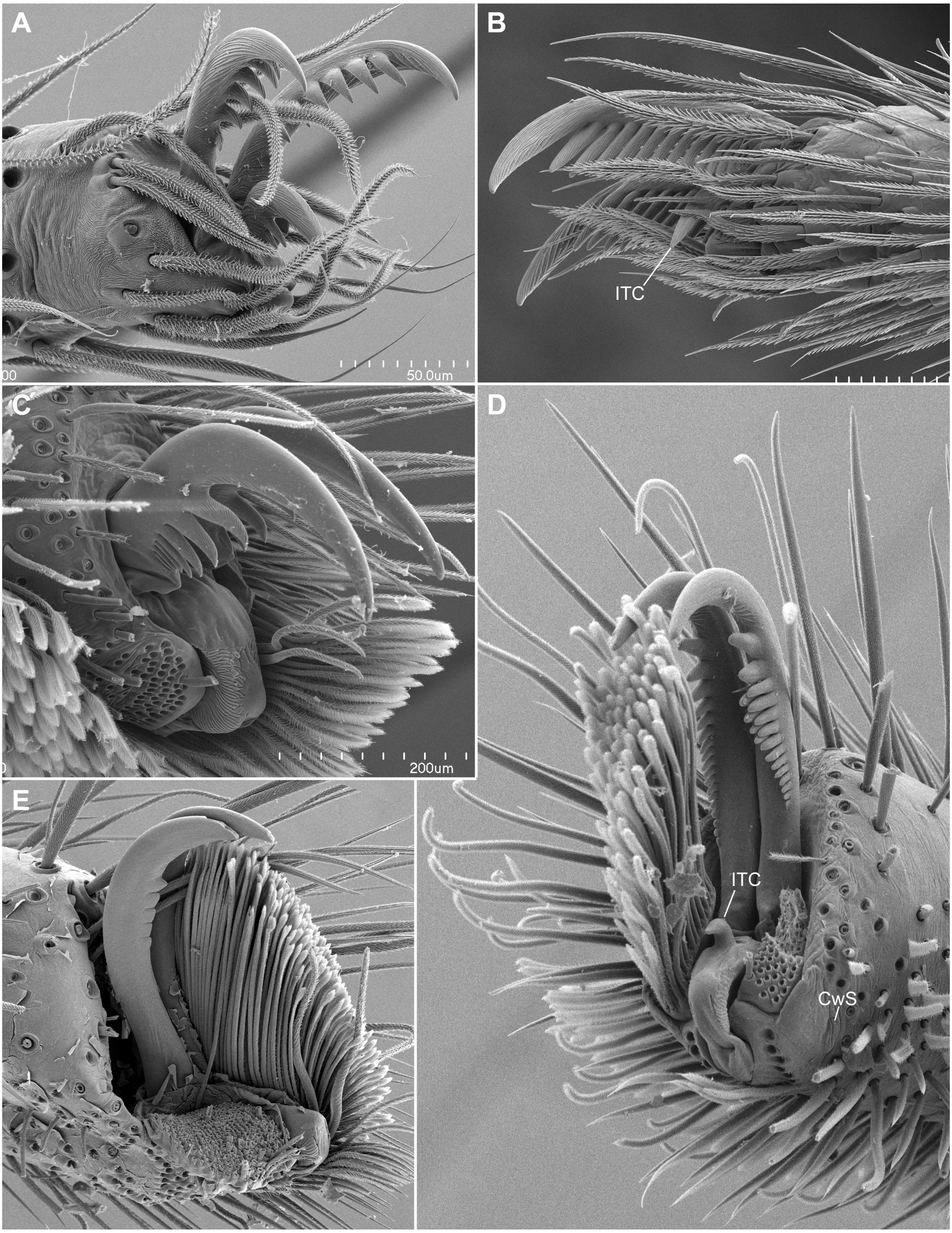


Fig. 62. Claws and claw tufts, female. **A.** *Toxopsiella minuta* (Cycloctenidae), left IV, apical. **B.** *Oxyopes heterophthalmus* (Oxyopidae), right I, prolateral-ventral. **C.** *Lauricius hooki* (Tengellidae) left I, retrolateral-apical. **D.** *Liocranoides unicolor* (Tengellidae), left I, apical. **E.** *Selenops debilis* (Selenopidae), left I, prolateral.

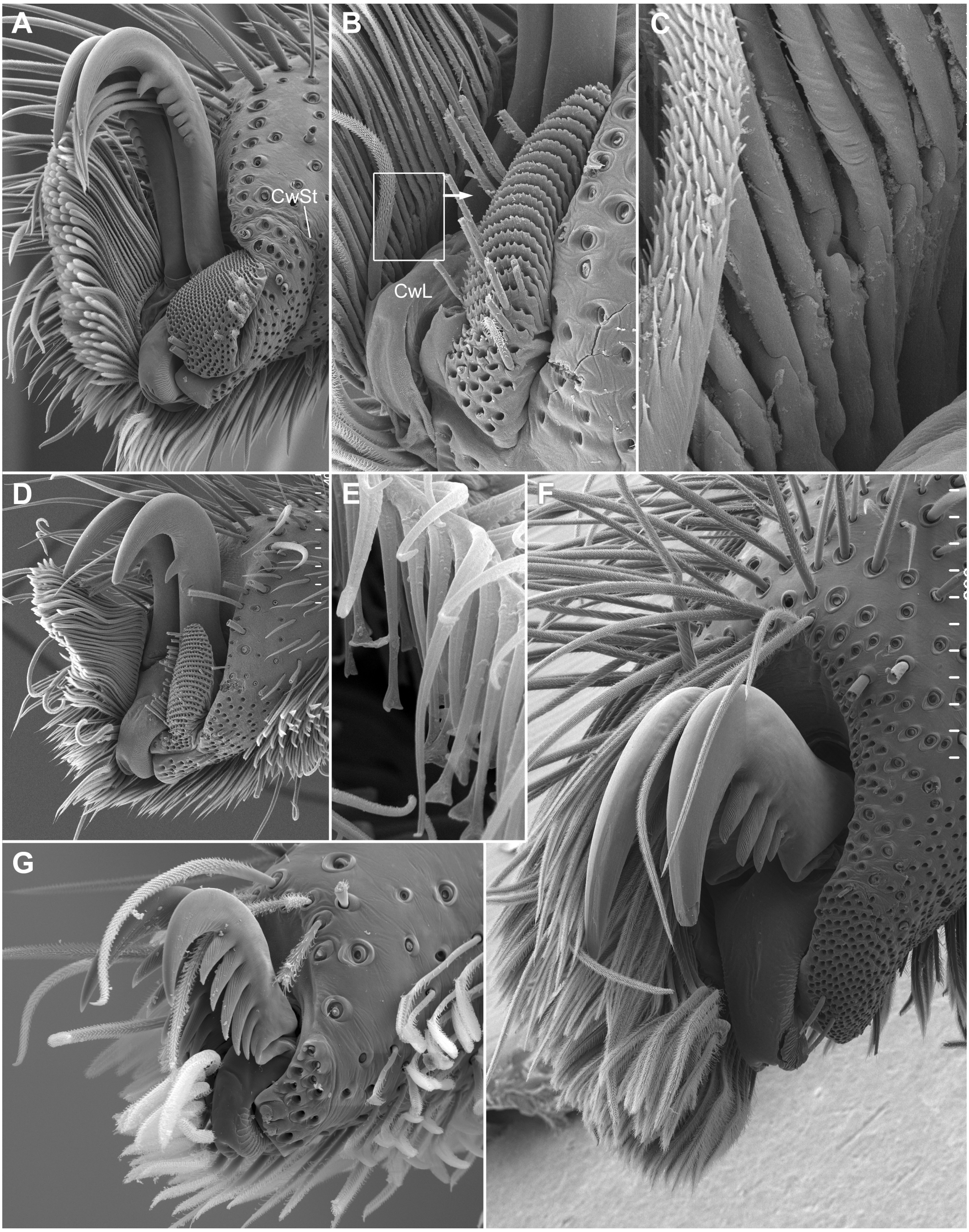


Fig. 63. Claws and claw tufts, left, female. **A.** *Vulsor* sp. (Ctenidae), claws I apical-retrolateral. **B.** *Acanthoctenus* cf. *spinipes* (Ctenidae), base of claw tuft, apical-retrolateral, marked inset in C. **C.** Same, detail of insertions of claw tuft setae. **D.** *Ctenus* cf. *crulsi* (Ctenidae), claws I apical-retrolateral. **E.** *Macerio flavus* (Miturgidae), detail tenent barbs on claw tuft seta IV. **F.** *Miturga* cf. *lineata* (Miturgidae), claws I apical-retrolateral. **G.** *Paravulsor* sp. (Eutichuridae), claws I apical-retrolateral.

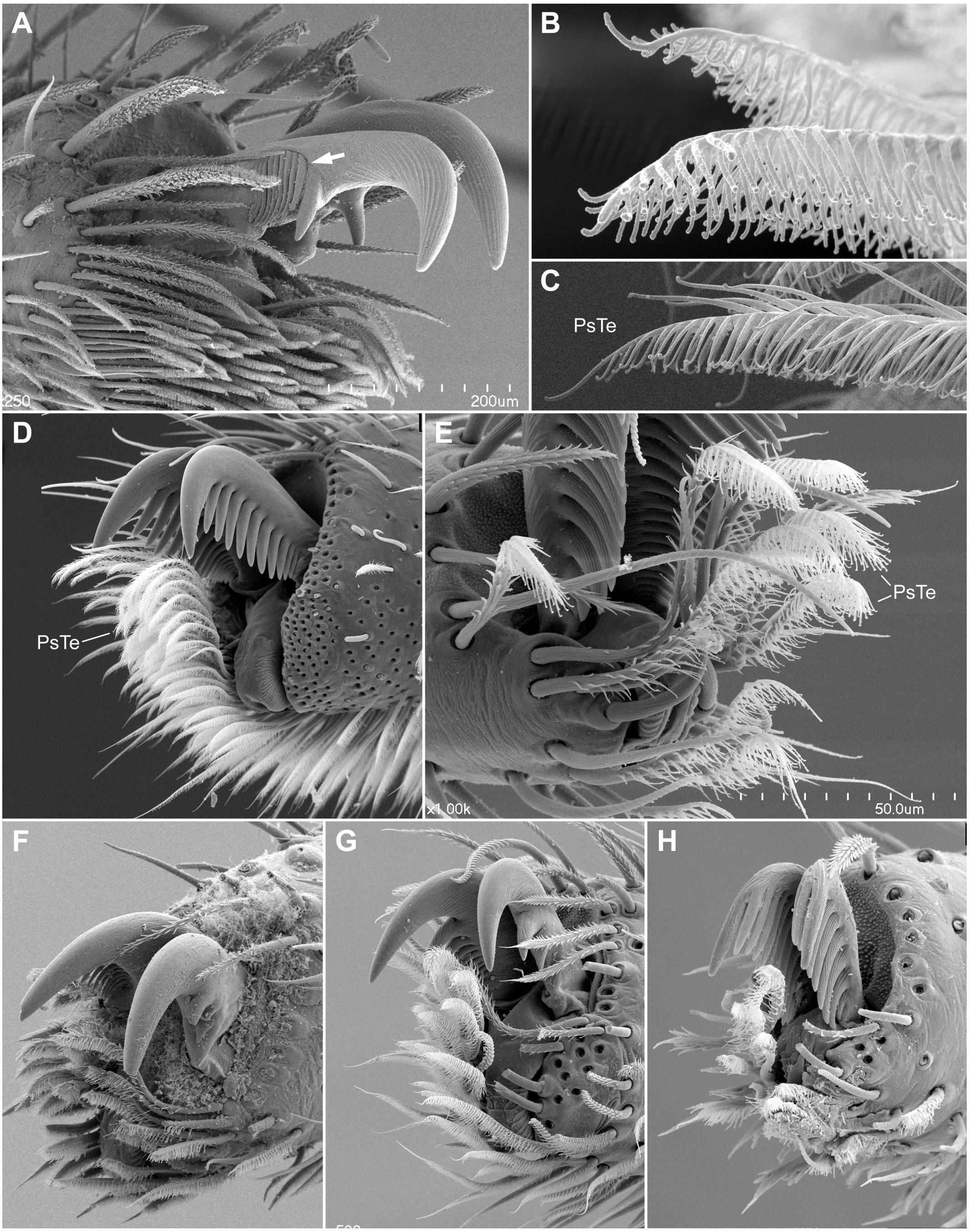


Fig. 64. Claws and claw tufts of Thomisidae, female (except H, male). **A.** *Borboropactus bituberculatus*, female, left claws IV, prolateral, arrow to patch of teeth on proclaw. **B.** Same, detail of pseudotenent seta. **C.** *Stephanopoides sexmaculata*, female, detail of pseudotenent seta. **D.** Same, left claws I, retrolateral-apical. **E.** *Titidius* sp., female, right claws I, retrolateral-apical. **F.** *Stephanopis ditissima* female, left claws I, retrolateral-apical. **G.** *Geraesta hirta*, female, left claws I, retrolateral-apical. **H.** *Strophius albofasciatus*, male, left claws I, prolateral-apical.

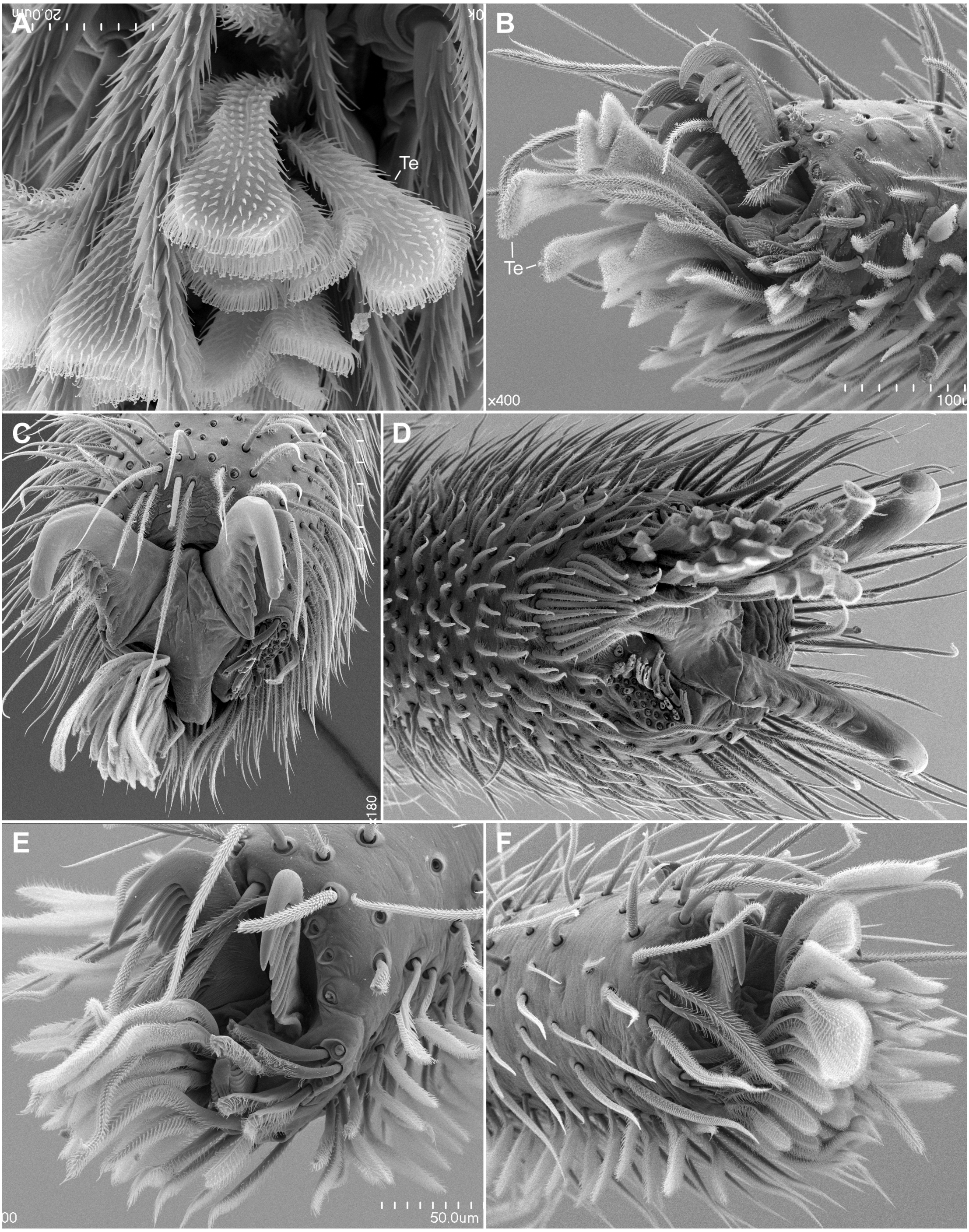


Fig. 65. Claws and claw tufts of Anyphaenidae, female. **A.** *Malenella nana*, claw tuft setae I, dorsal. **B.** *Anyphaena accentuata*, right claws I, prolateral. **C.** *Amaurobioides africana*, left claws IV, apical. **D.** Same, ventral. **E.** *Gayenna americana*, left claws I, retrolateral-apical. **F.** Same, left claws IV, prolateral-apical.

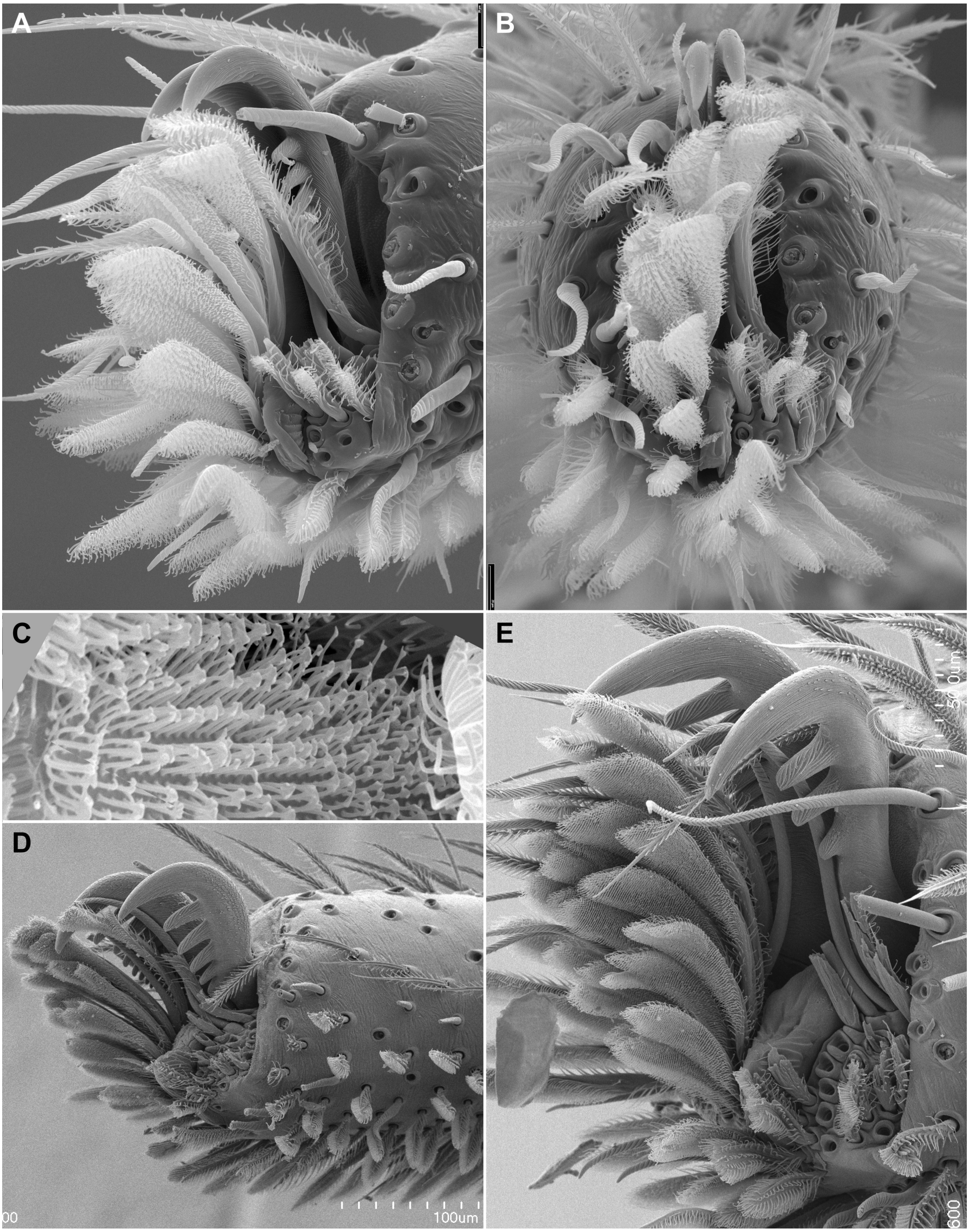


Fig. 66. Claws and claw tufts of Philodromidae, female left leg I. **A.** *Titanebo mexicanus*, retrolateral-apical. **B.** Same, apical. **C.** Same, detail of tenent barbs of claw tuft seta. **D.** *Philodromus aureolus*, retrolateral. **E.** Same, detail retrolateral-apical.

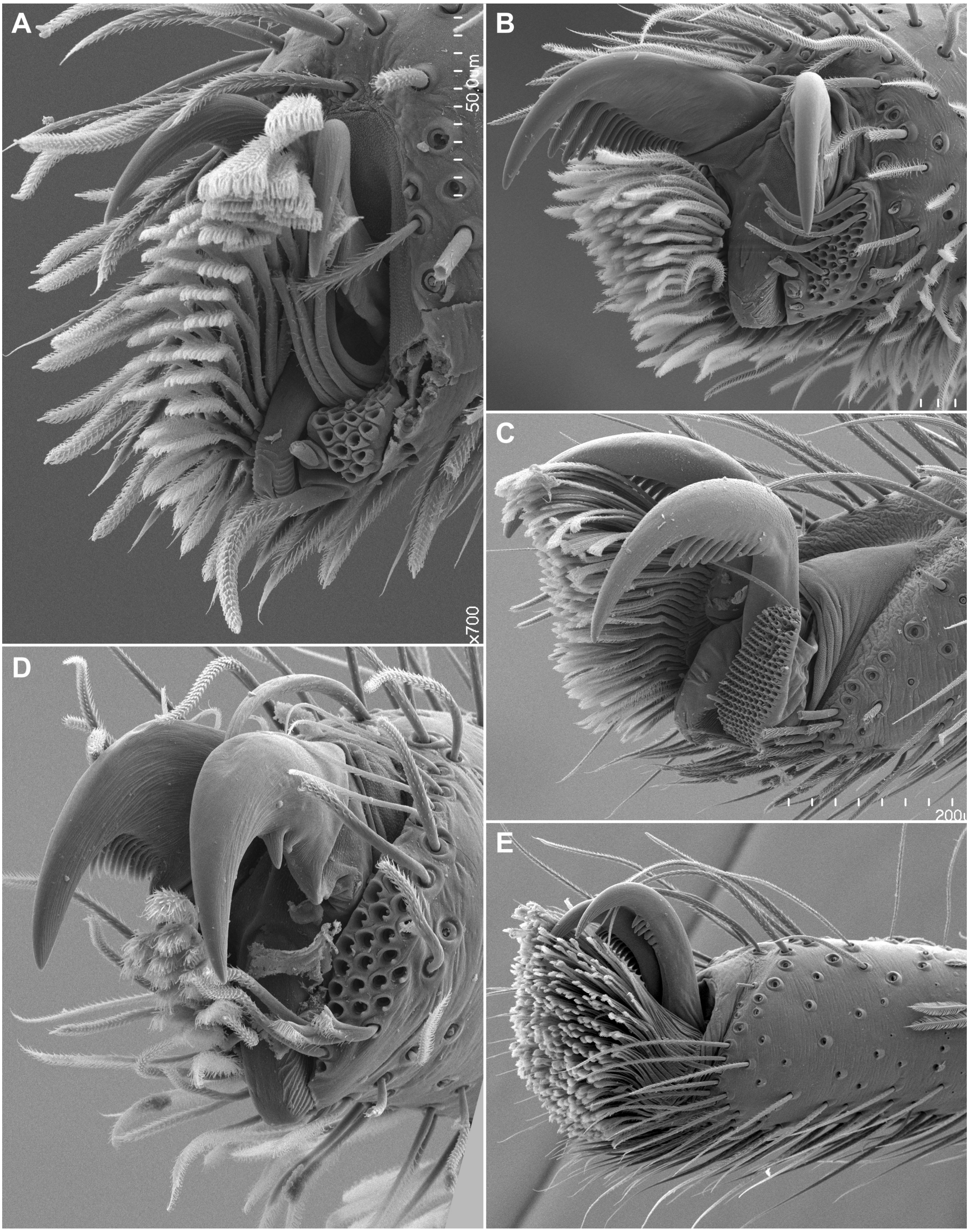


Fig. 67. Claws and claw tufts of female, left side. **A.** *Donuea* sp. ("Liocranidae"), I, retrolateral-apical. **B.** *Clubiona pallidula* (Clubionidae), I, retrolateral-apical. **C.** *Cocalodes longicornis* (Salticidae), I, retrolateral-apical. **D.** *Hispo* sp. (Salticidae), I, retrolateral-apical. **E.** *Holcolaetis* cf. *zuluensis* (Salticidae), IV, retrolateral.

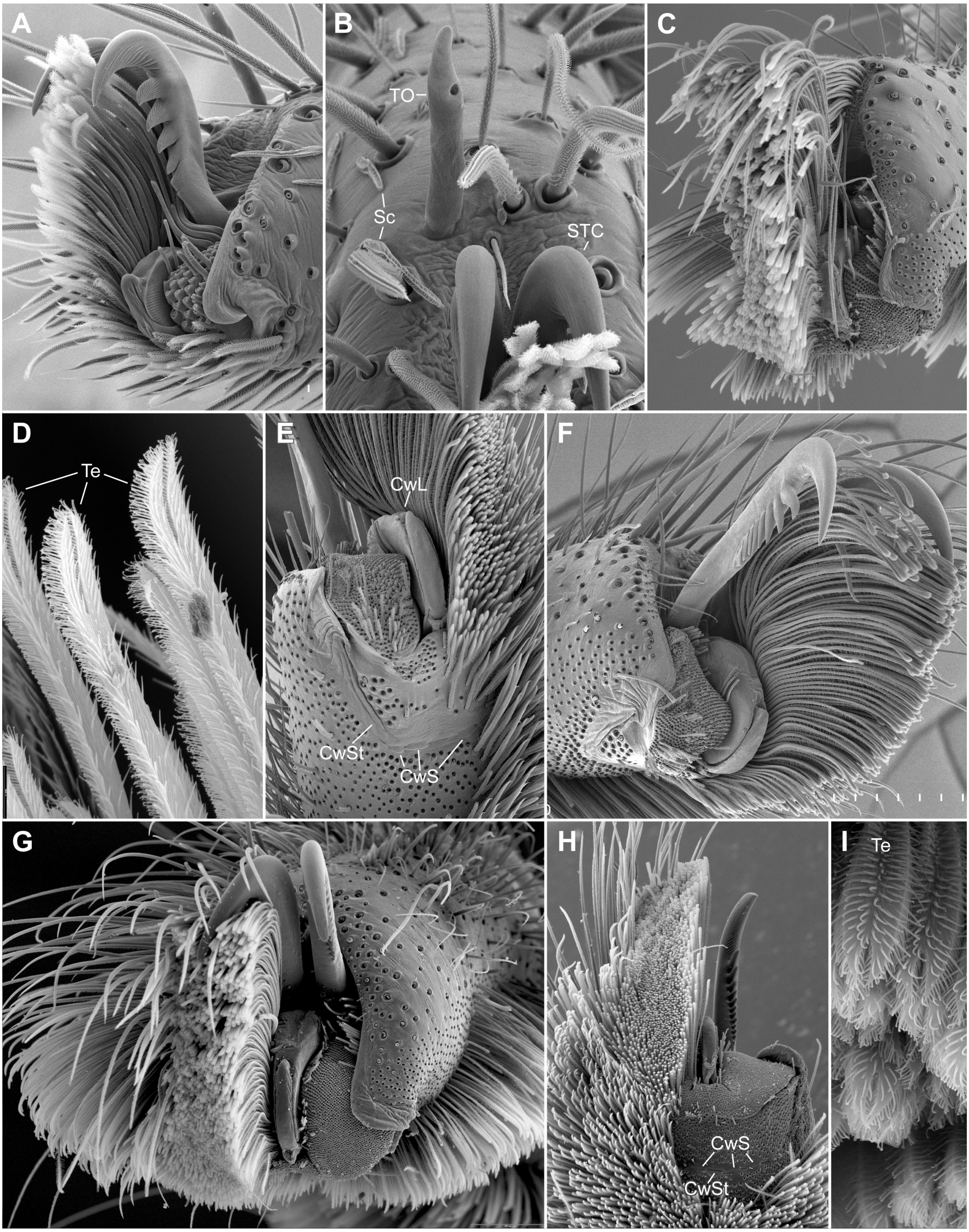

A
B
TO
Sc
STC
C
D
Te
E
CwL
CwSt
CwS
F
G
H
CwS
CwSt
I
Te

Fig. 68. Claws and claw tufts of Sparassidae, female, left side. **A.** Sparianthinae VEN, I, retrolateral. **B.** Same, tarsal organ, apical. **C.** *Eusparassus* cf. *walckenaeri*, IV, apical. **D.** Same, tips of claw tuft setae. **E.** *Heteropoda venatoria*, IV, ventral. **F.** Same, prolateral-apical. **G.** *Polybetes pythagoricus*, IV, apical. **H.** Same, ventral. **I.** Same, tips of claw tuft setae.

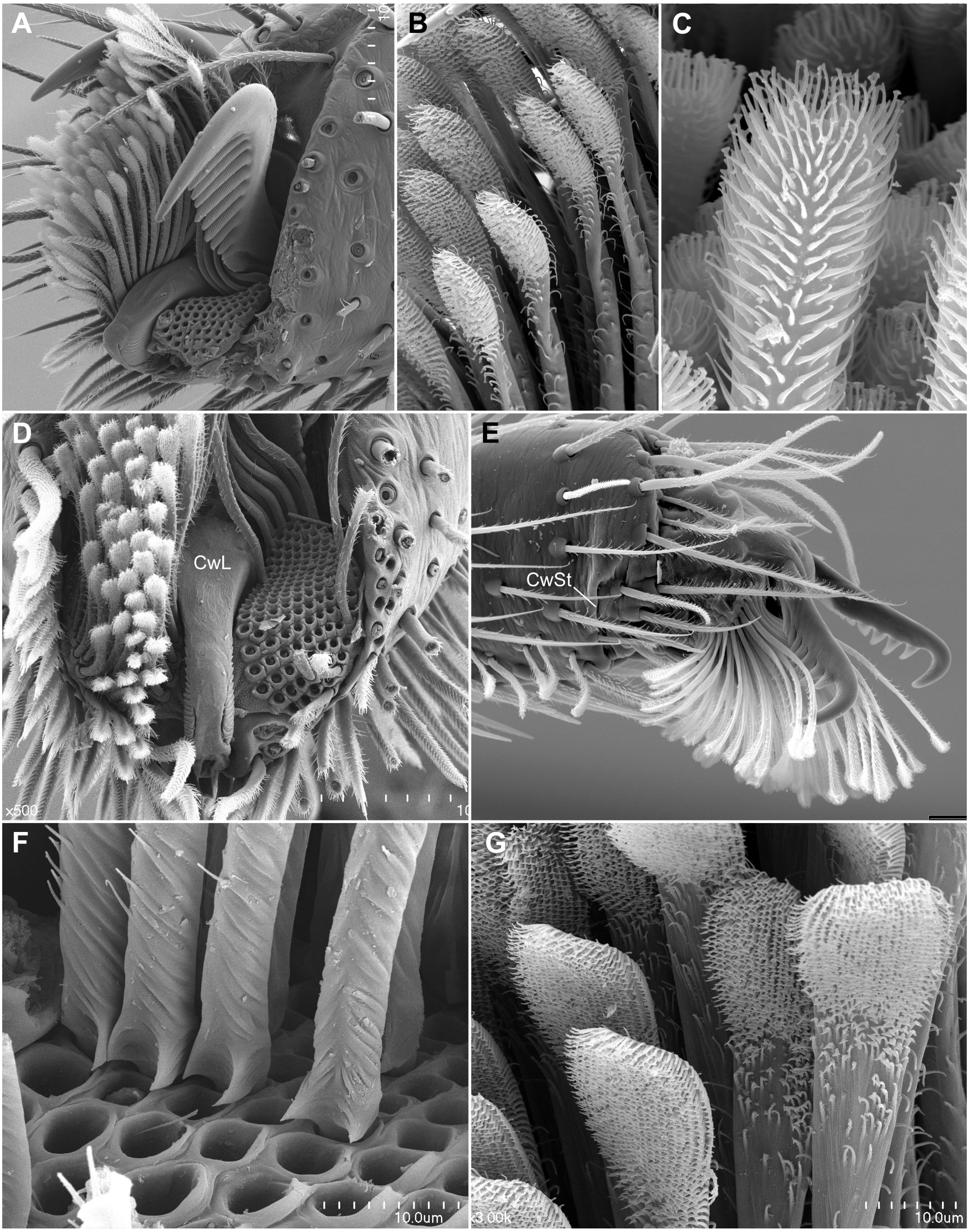


Fig. 69. Claws and claw tufts of Corinnidae, female, left side. **A.** *Corinna* cf. *bulbula*, claws I, retrolateral-apical. **B.** Same, claw tuft setae. **C.** *Paradiestus penicillatus*, tips of claw tuft setae IV. **D.** *Mandaneta sudana*, claw lever and base of claw tuft I. **E.** *Castianeira trilineata*, claws IV, prolateral. **F.** *Copa flavoplumosa*, base of claw tuft setae I. **G.** Same, tips of claw tuft setae.

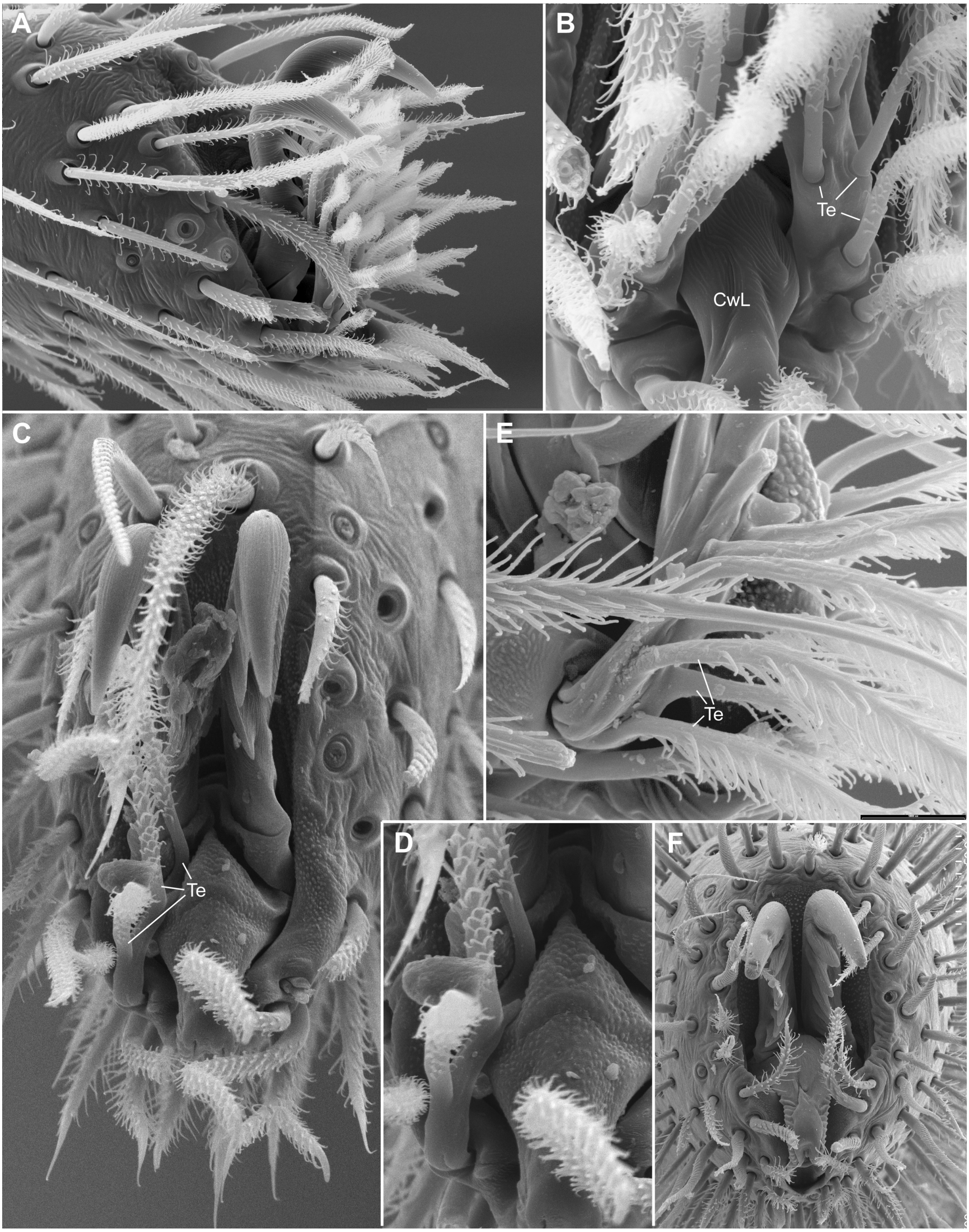


Fig. 70. Claws and claw tufts of the *Teutamus* group (Liocranidae), female, left side. **A.** *Oedignatha* cf. *jocquei*, claws I, prolateral-apical. **B.** Same, detail of claw tuft base, apical. **C.** *Teutamus* sp., claws I, apical. **D.** Same, detail of law tuft base. **E.** Same, claw tuft setae IV with fused bases, prolateral. **F.** *Sesieutes* sp., claws I, apical.

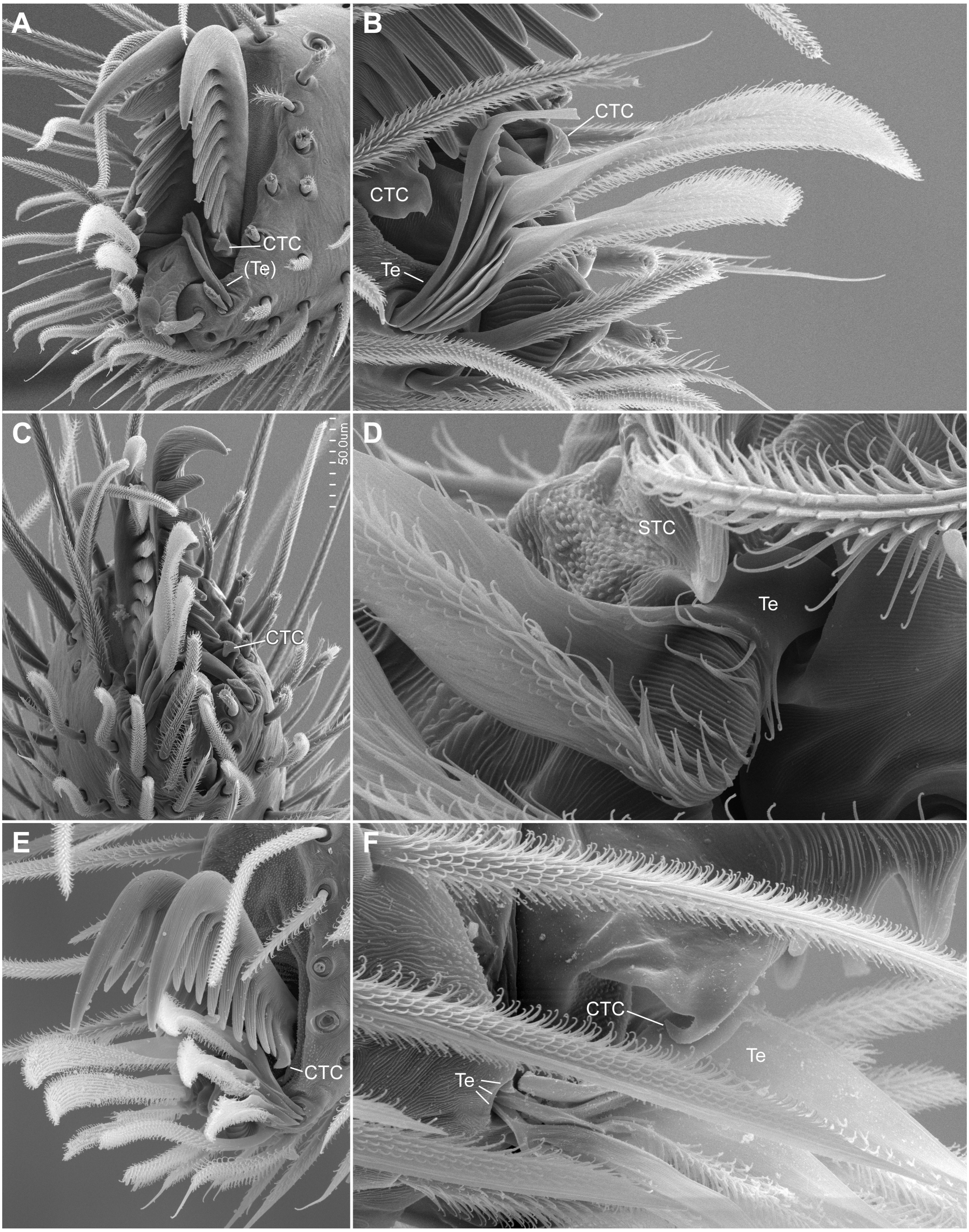

A
CTC
(Te)
B
CTC
CTC
Te
C
50.0um
CTC
D
STC
Te
E
CTC
F
CTC
Te
Te

Fig. 71. Claws and claw tufts of representatives usually placed in Liocranidae, female, left side. **A.** *Toxoniella* sp., claws I retrolateral-apical. **B.** Same, claw tuft and base of claw, prolateral. **C.** Same, claws apical. **D.** *Apostenus californicus*, base of claw tuft seta and of claw I, retrolateral. **E.** Cf. Liocranidae LIB, claws I retrolateral-apical. **F.** Same, base of claw tuft seta and of claw IV, prolateral.

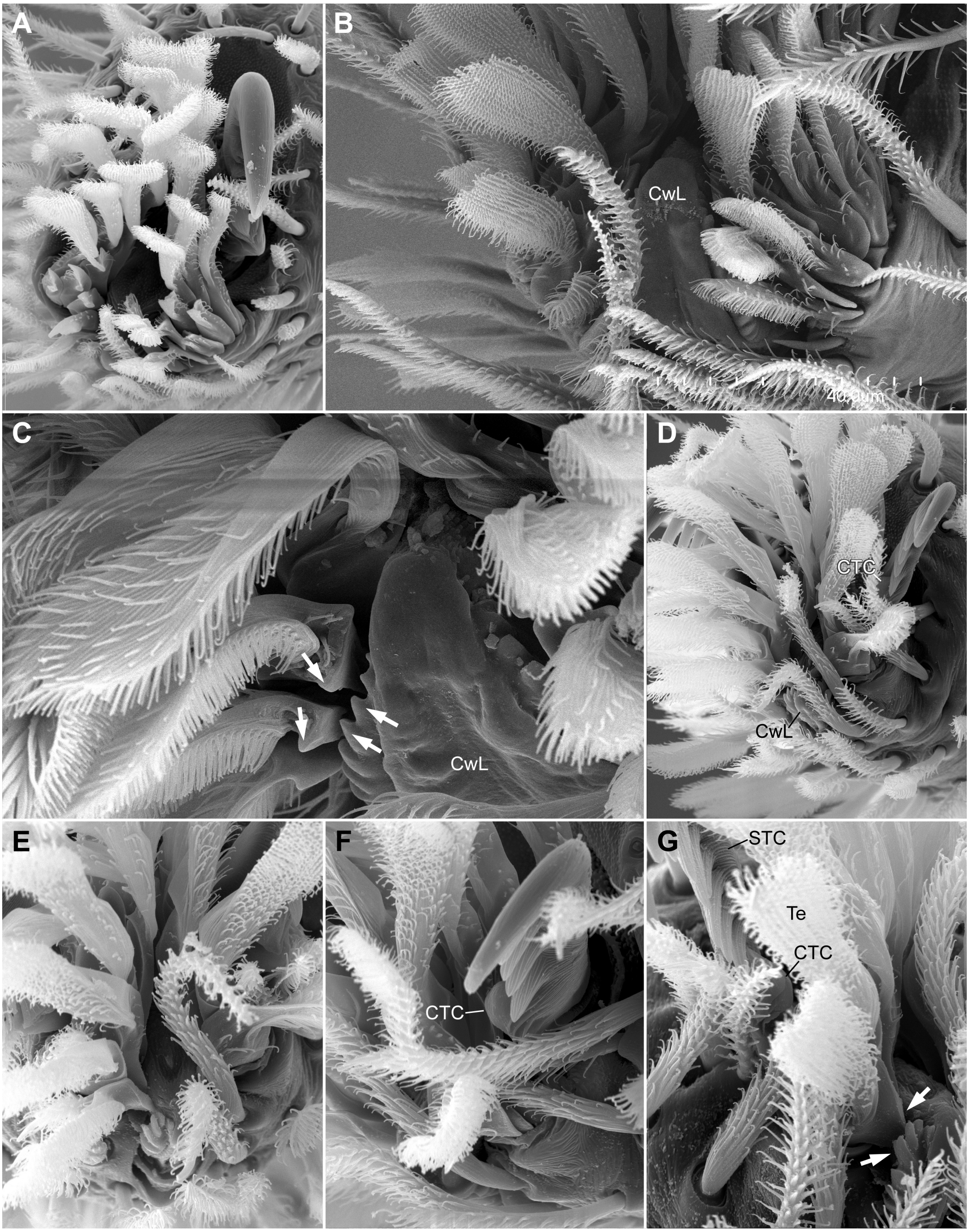


Fig. 72. Claws and claw tufts of Trachelidae, female; white arrows to enlarged ridges in the claw lever and corresponding expanded setal bases. **A.** *Meriola barrosi*, left I, apical. **B.** Same, right IV, apical. **C.** Same, left IV, apical. **D.** *Trachelas minor*, left I, apical. **E.** Same, detail of claw lever and claw tuft. **F.** Same, detail of retroclaw and claw tuft. **G.** Same, detail of proclaw, claw lever and claw tuft.

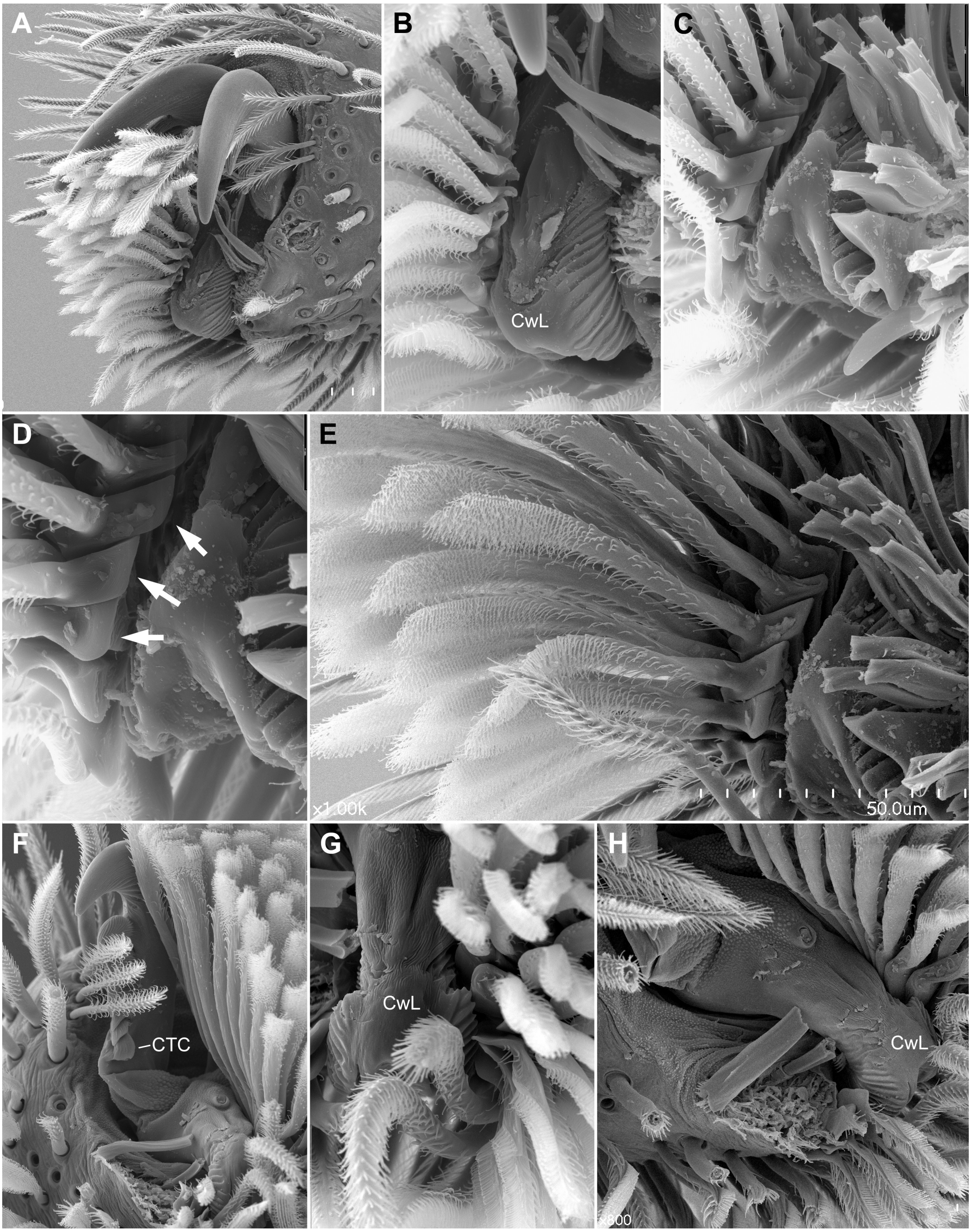


Fig. 73. Claws and claw tufts of Trachelidae, female, left side. Arrows to interlocking projections of claw lever and claw tuft setae. **A.** *Trachelas mexicanus*, claws I, retrolateral-apical. **B.** Same, detail. **C.** Same, claw tuft base and claw lever IV. **D.** Same, detail, arrows to rectangular block-shaped setal bases. **E.** Same, claw tuft. **F.** *Trachelopachys ammobates*, proclaw II and claw tuft. **G.** Same, detail of claw tuft base and claw lever. **H.** Same, prolateral claw tuft pulled up.

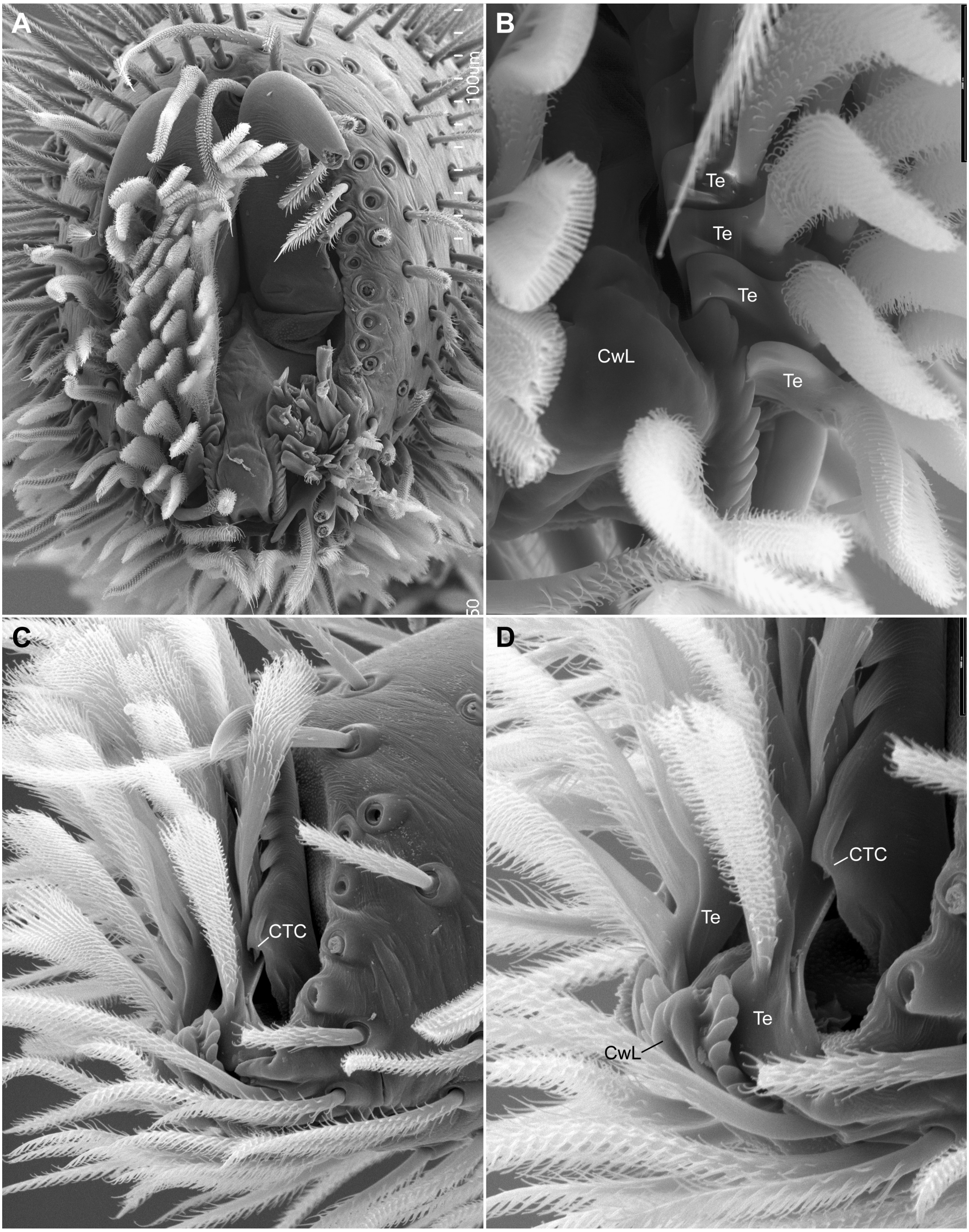

A
100µm
50
B
Te
Te
Te
CwL
Te
C
CTC
D
CTC
Te
Te
CwL

Fig. 74. Claws and claw tufts of Trachelidae, female, left side. **A.** *Paccius* cf. *scharffi*, claws I, apical. **B.** Same, detail of interlocking claw tuft base and claw lever IV. **C.** Trachelidae ARG, claws I, retrolateral-apical. **D.** Same, claw tuft base and claw lever IV, apical.

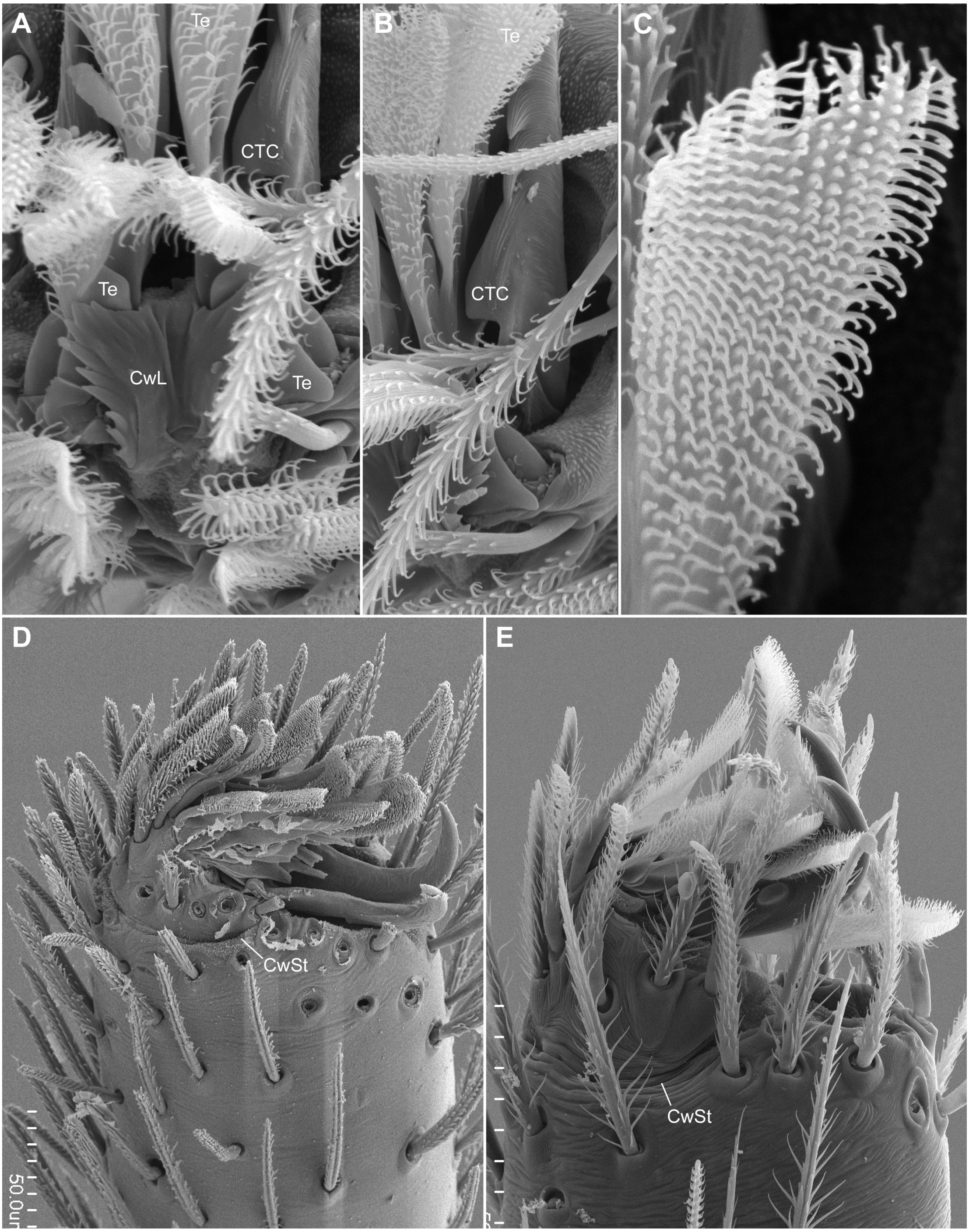


Fig. 75. Claws and claw tufts of Trachelidae and Phrurolithidae, female, left side. **A.** Trachelidae ARG, claw tuft base and claw lever IV, apical. **B.** Same, detail of claw–claw tuft clasping mechanism and fused setae. **C.** Same, tenent surface of claw tuft seta from leg I. **D.** *Drassinella gertschi*, claws I, retrolateral. **E.** *Phrurolithus festivus*, claws I, retrolateral.

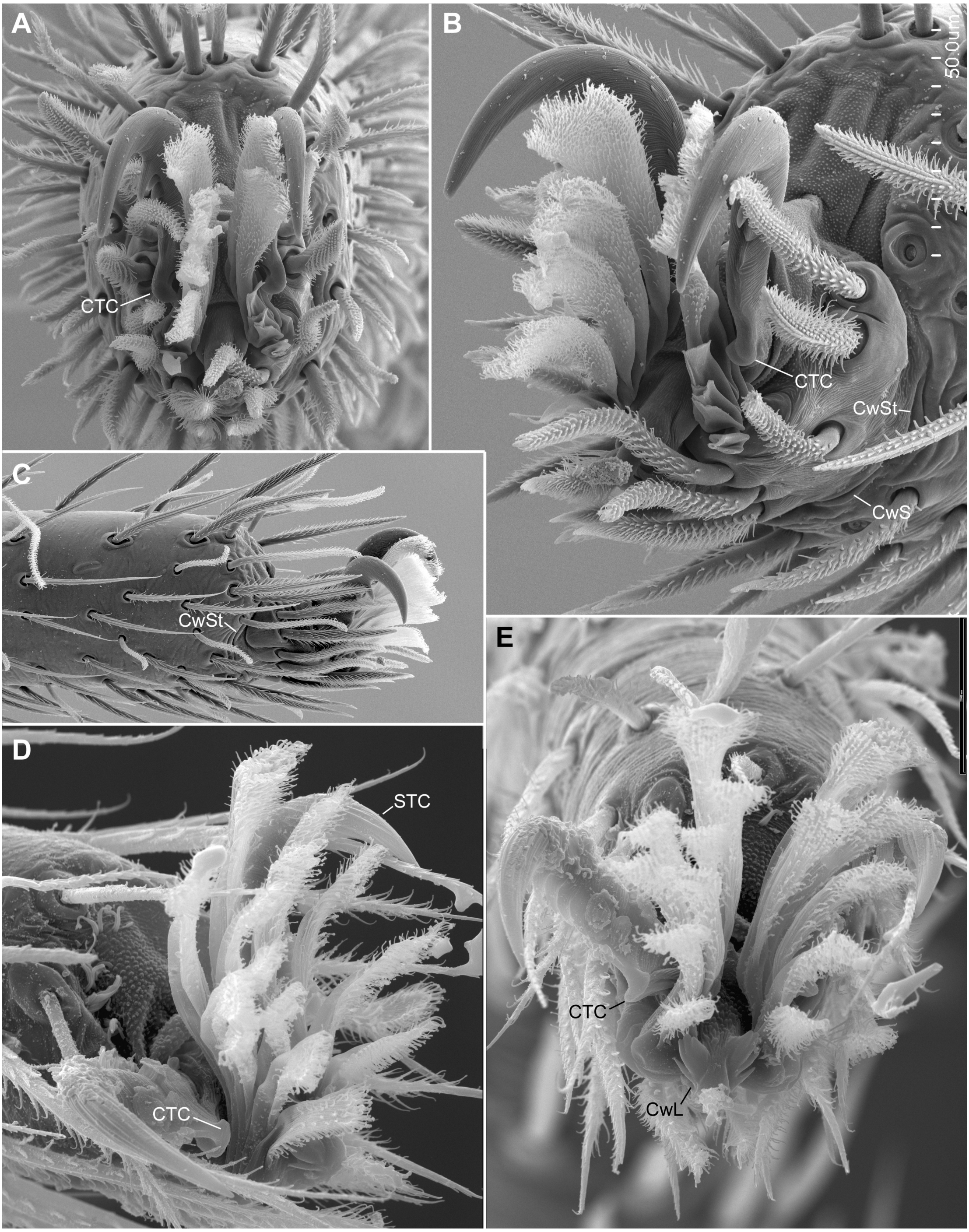

A
CTC
B
50.0um
CTC
CwSt
CwS
C
CwSt
D
STC
CTC
E
CTC
CwL

Fig. 76. Claws and claw tufts I of Phrurolithidae, female, left side. **A.** *Otacilia* sp., apical. **B.** Same, retrolateral-apical. **C.** Same, prolateral. **D.** *Orthobula calceata*, retrolateral-apical. **E.** Same, apical.

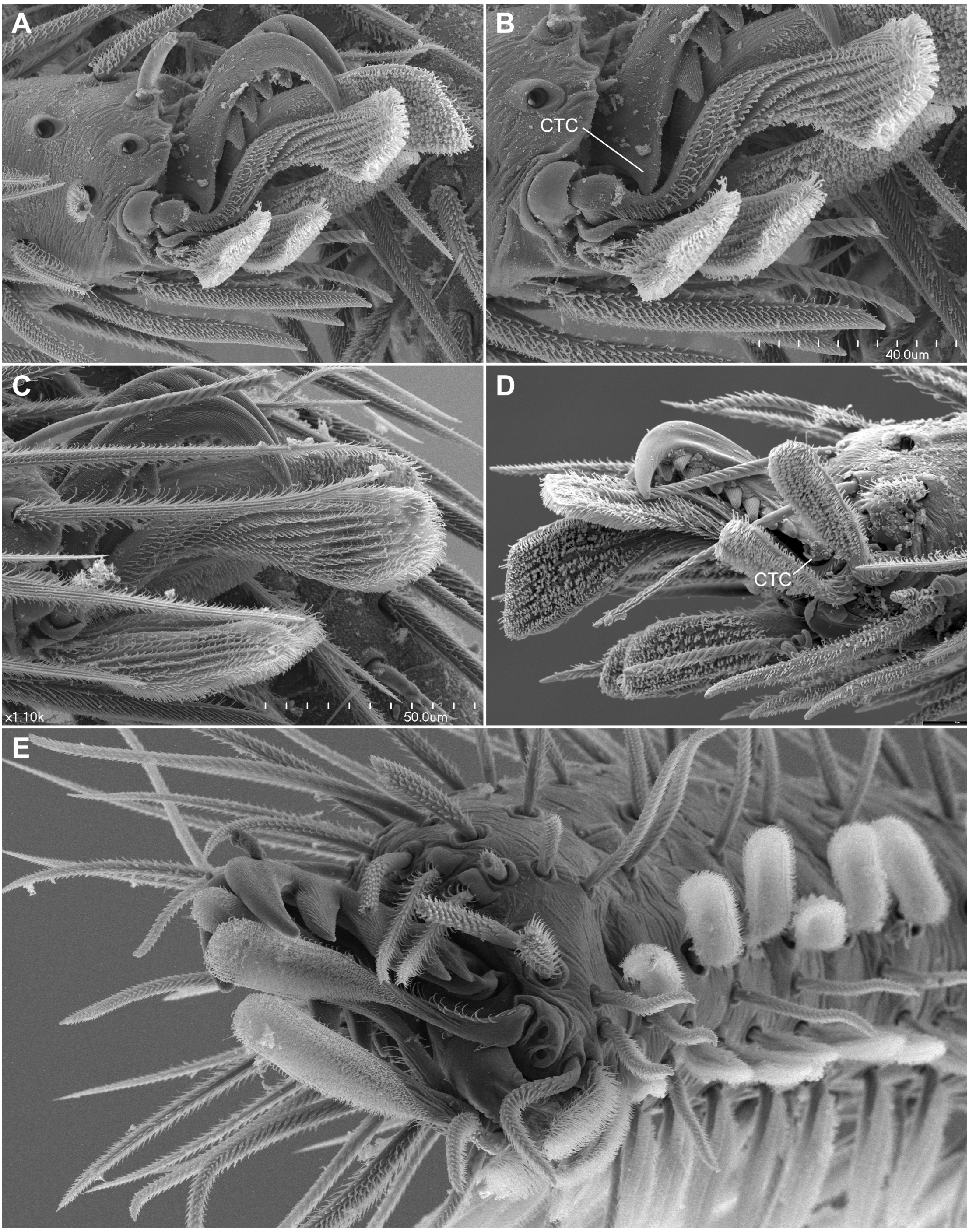


Fig. 77. Claws and claw tufts, female. **A.** *Ammoxenus coccineus* (Ammoxenidae), left, probably leg II, claws, prolateral-apical. **B.** Same, detail. **C.** Same, prolateral. **D.** Same, ventral. **E.** *Cithaeron delimbatus* (Cithaeronidae), right claws I, apical-ventral.

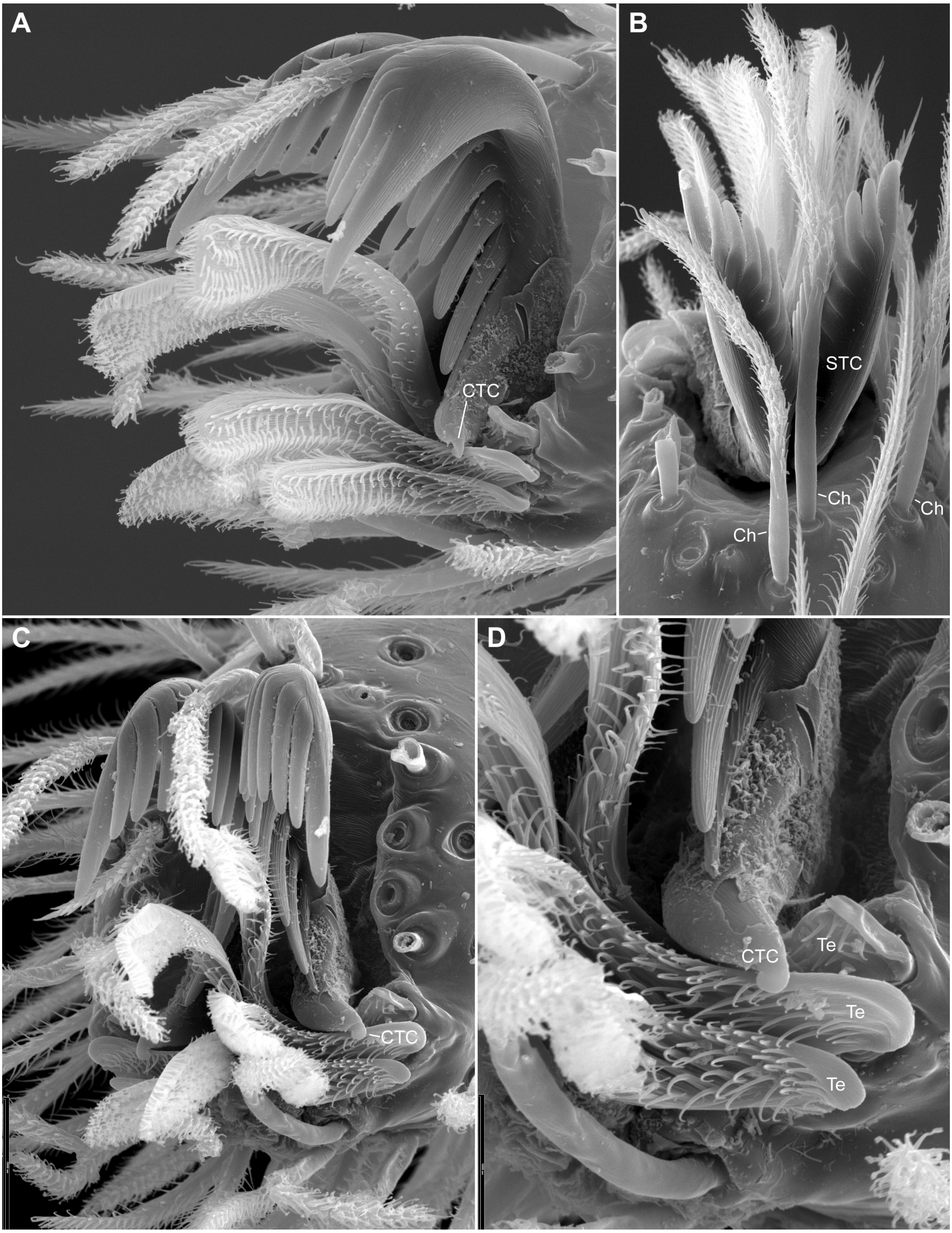

A
CTC
B
STC
Ch
Ch
Ch
C
CTC
D
CTC
Te
Te
Te

Fig. 78. Claws and claw tufts I of *Rastellus florisbad* (Ammoxenidae), female, left side. **A.** Retrolateral-apical. **B.** Dorsal. **C.** Apical. **D.** Apical, detail of claw–claw tuft clasping mechanism.

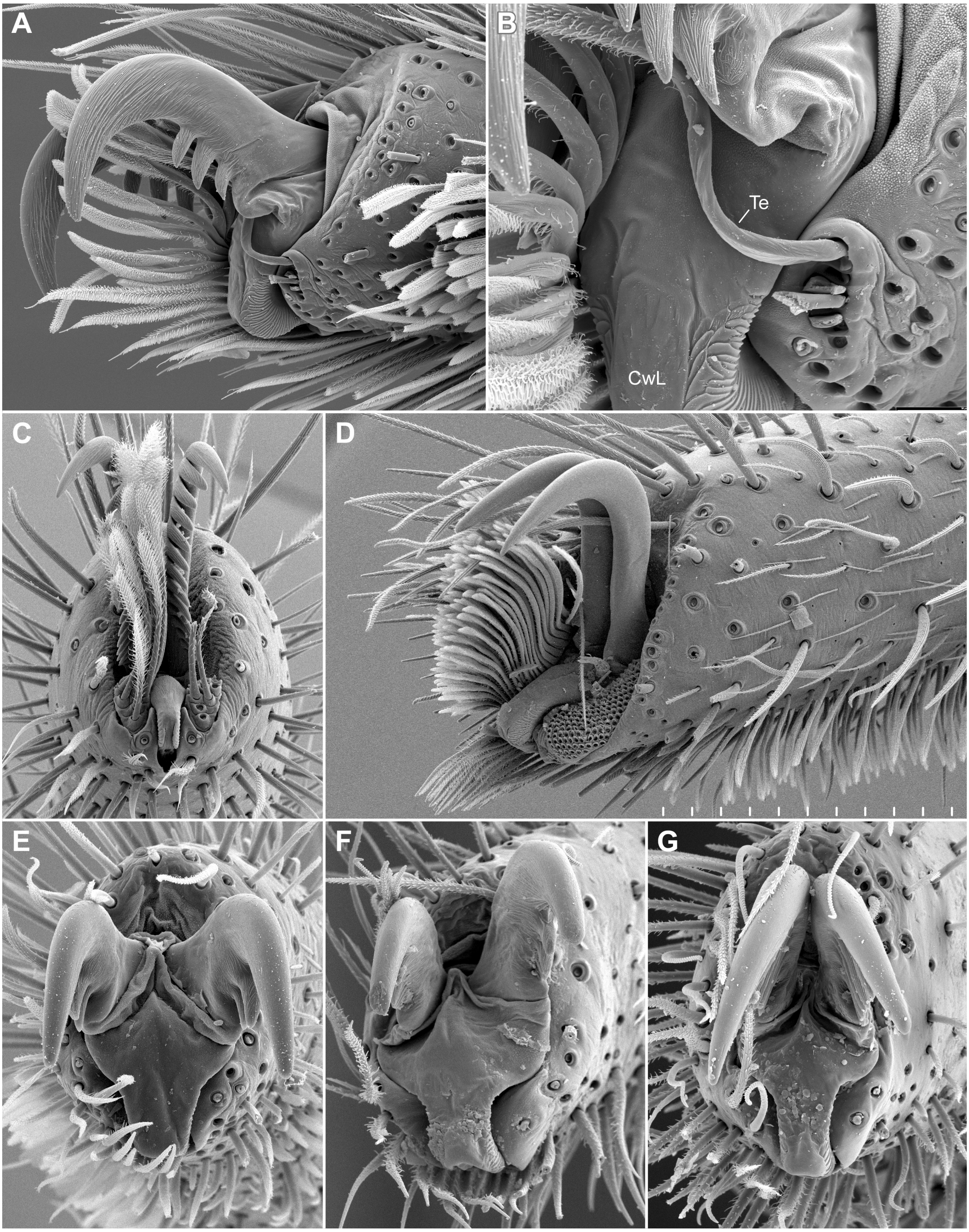


Fig. 79. Claws and claw tufts of female, left side. **A.** *Austrachelas pondoensis* (Gallieniellidae), claws IV, retrolateral. **B.** Same, detail of claw tuft base. **C.** *Desognaphosa yabbra* (Trochanteriidae), claws I, apical. **D.** *Fissarena castanea* (Trochanteriidae), claws I, retrolateral-apical. **E.** *Platyoides walteri* (Trochanteriidae), claws I, apical. **F.** *Doliomalus cimicoides* (Trochanteriidae), claws IV, apical. **G.** *Vectius niger* (Gnaphosidae), claws I, apical.

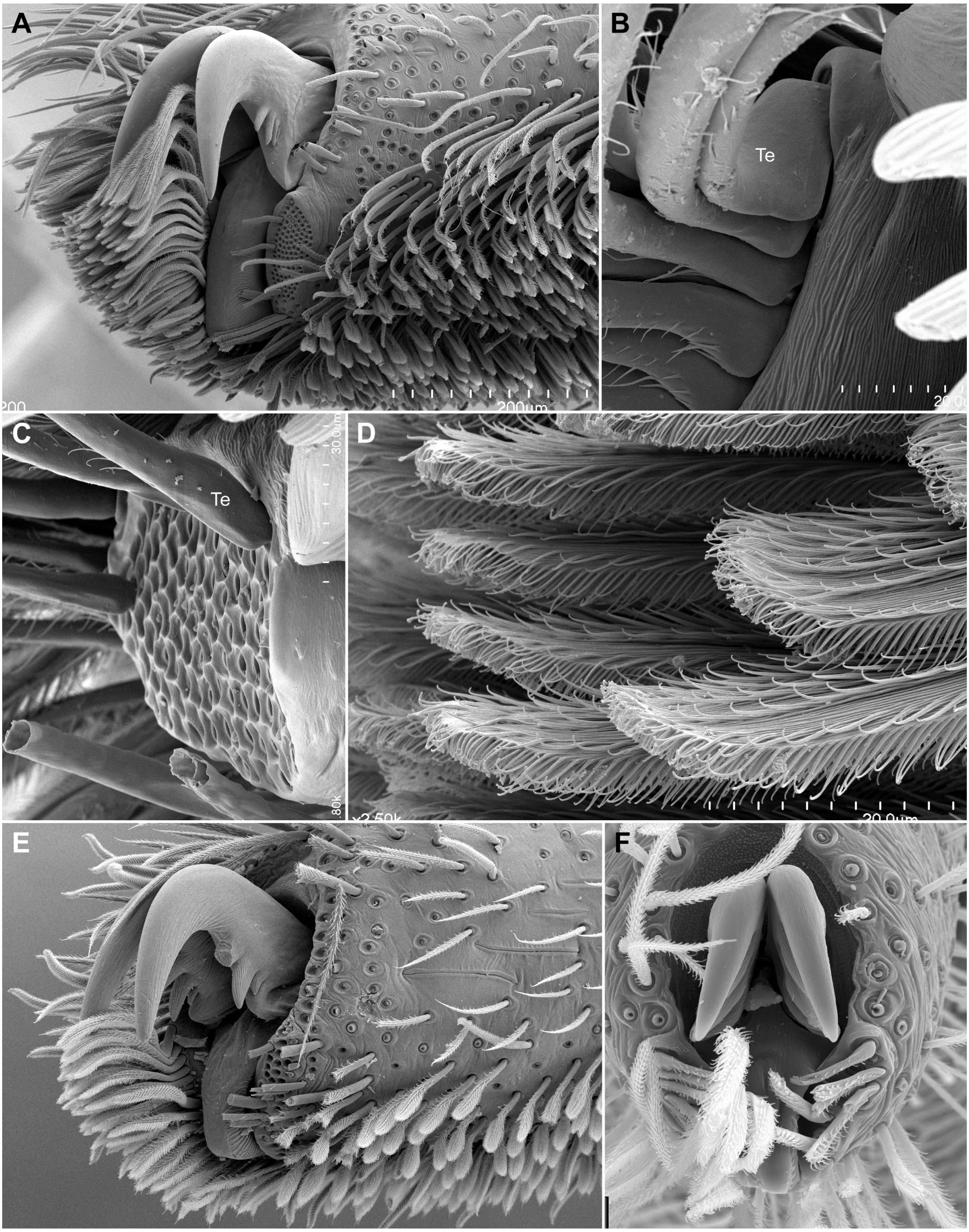


Fig. 80. Claws and claw tufts of Lamponidae, female. **A.** *Lampona cylindrata*, right claws I, prolateral-apical. **B.** Same, base of claw tuft setae, retrolateral setal pad. **C.** Same, insertion of claw tufts, prolateral setal pad. **D.** Same, detail of tips of claw tuft setae. **E.** *Centrothele mutica*, left claws I or II, retrolateral-apical. **F.** *Lamponella brookfield*, left claws I, apical.

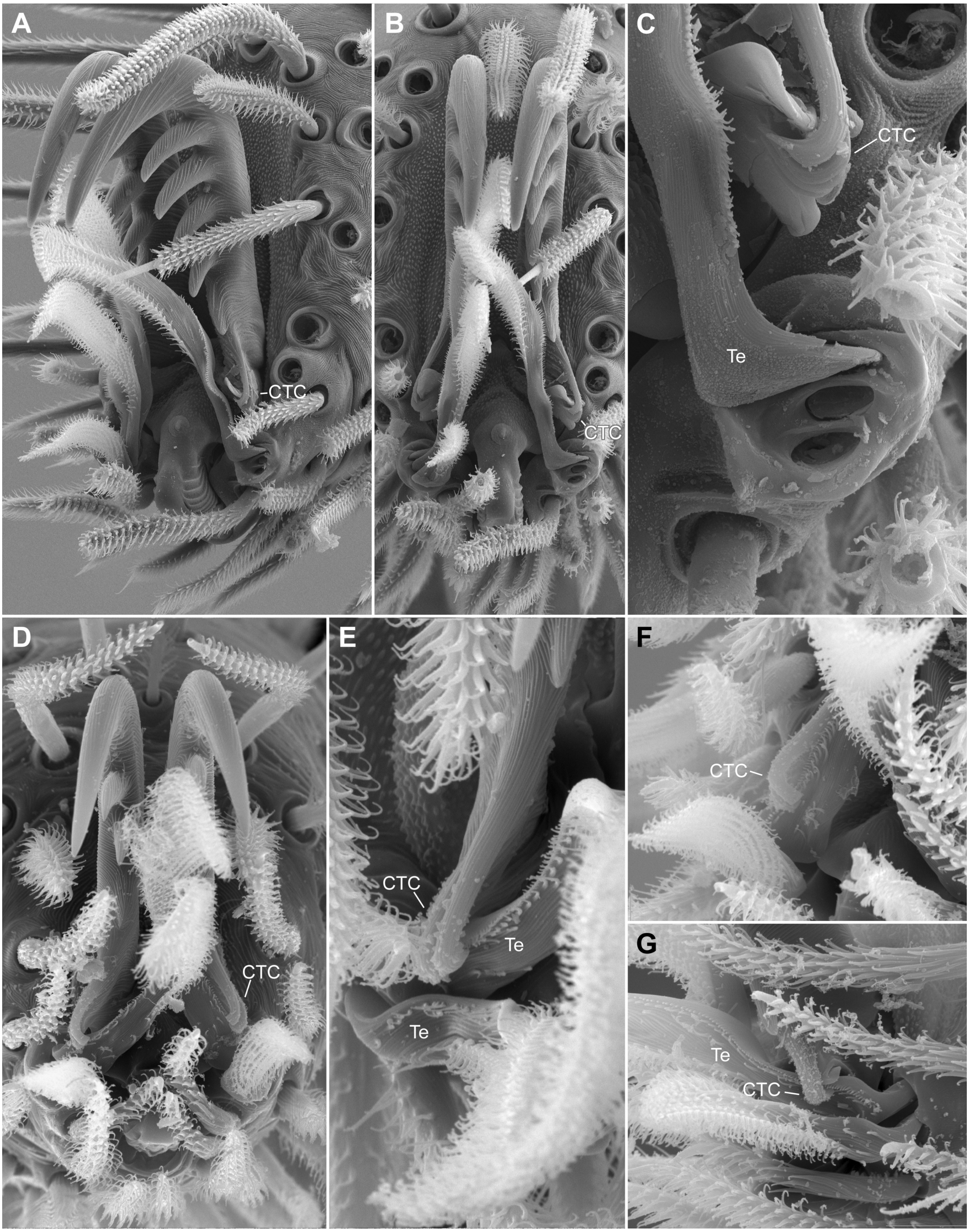

A
CTC
B
CTC
C
CTC
Te
D
CTC
E
CTC
Te
Te
F
CTC
G
Te
CTC

Fig. 81. Claws and claw tufts of Prodidomidae, female. **A.** *Lygromma* sp., right claws I, retrolateral-apical. **B.** Same, apical. **C.** Same, detail of claw–claw tuft clasper. **D.** Cf. *Moreno* ARG., left claws I, apical. **E.** Same, left proclaw III, detail of claw–claw tuft clasper. **F.** Same, right retroclaw I. **G.** Same, right proclaw II.

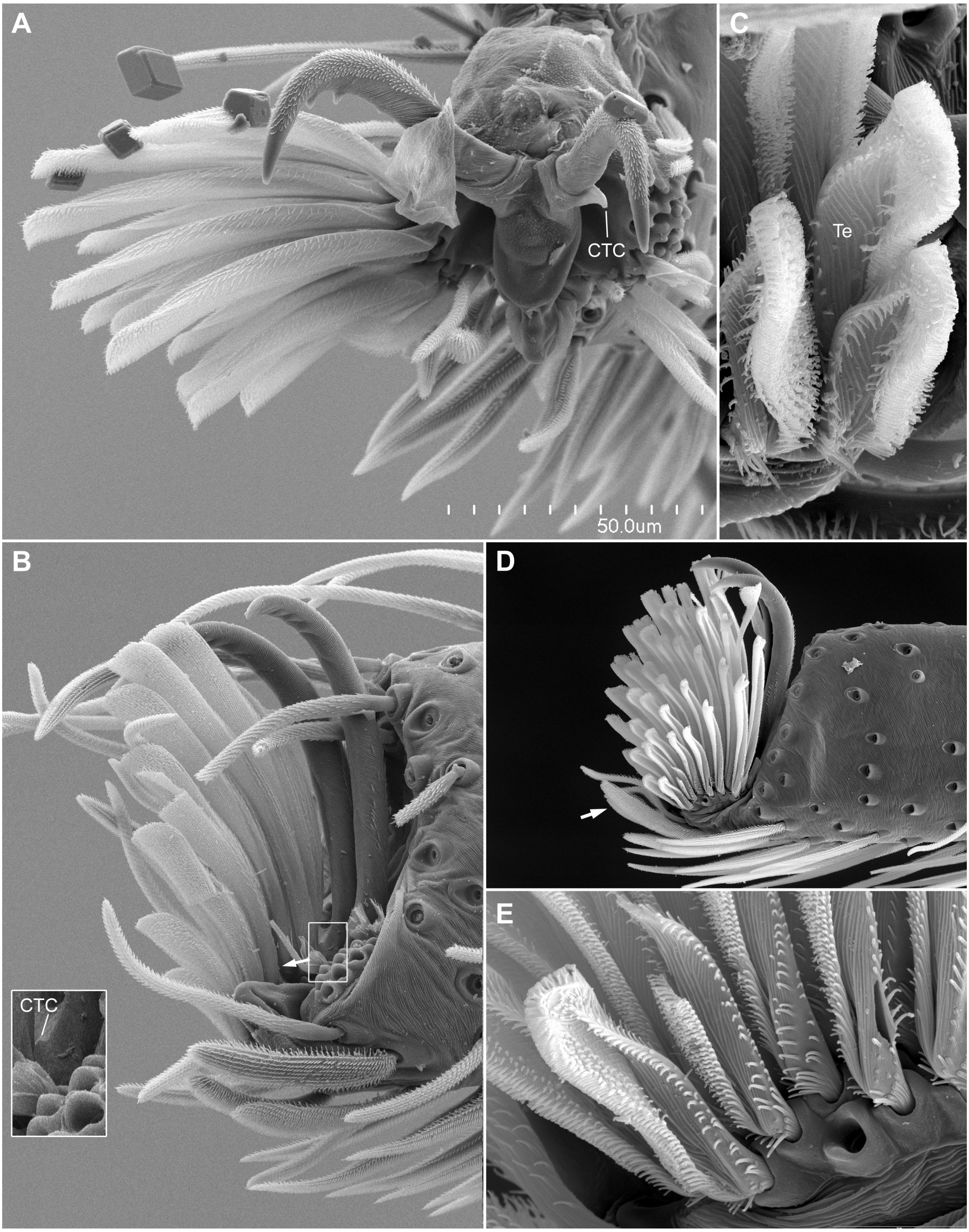


Fig. 82. Claws and claw tufts of Prodidominae, left side, female. **A.** *Neozimiris pubescens*, claws I, apical. **B.** *Prodidomus redikorzevi*, claws I, retrolateral, inset to base of retroclaw. **C.** Same, claw tuft setae. **D.** Same, claws IV, retrolateral, arrow to thick setae. **E.** Same, detail of claw tuft.

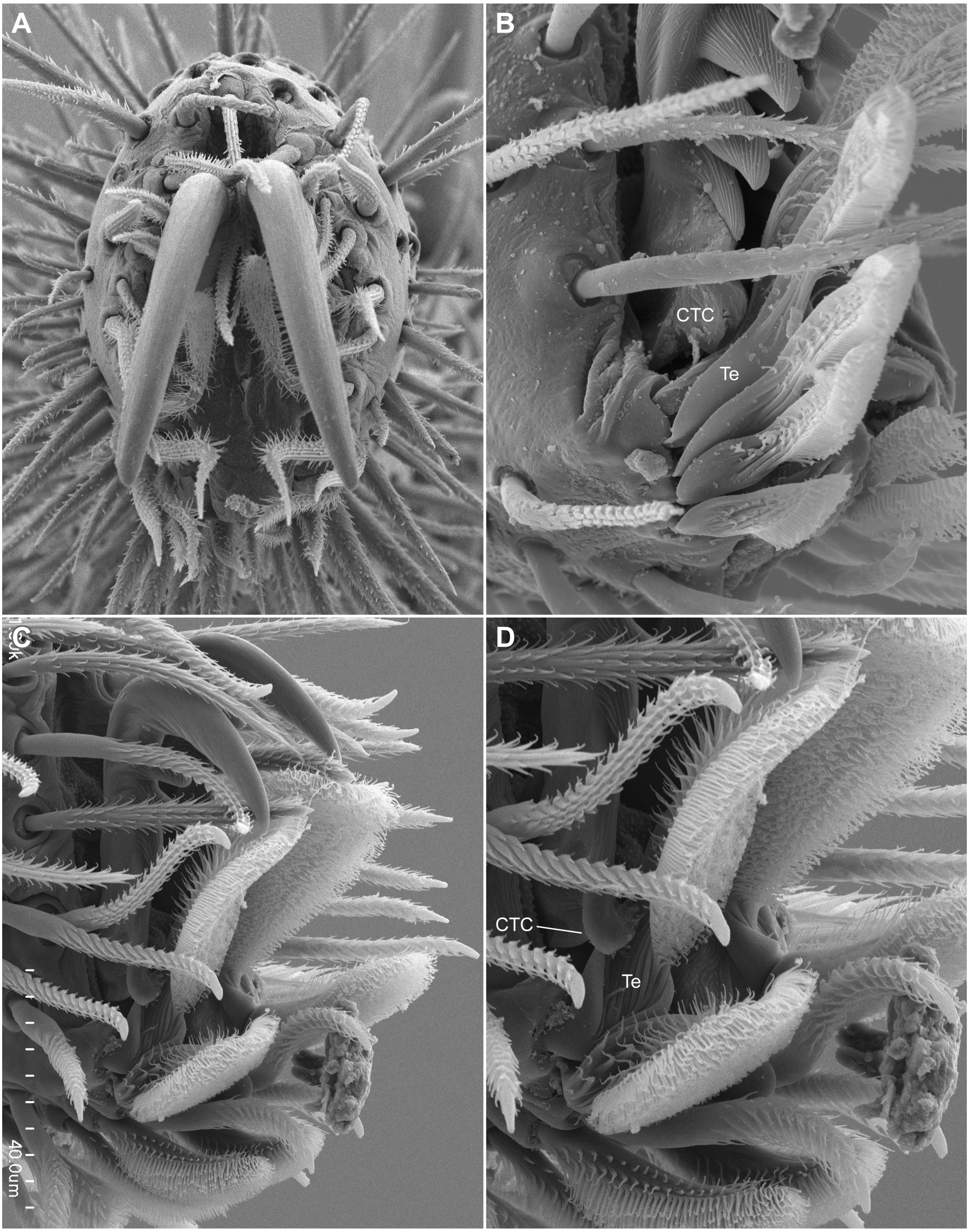


Fig. 83. Claws and claw tufts of Gnaphosidae, left side, female. **A.** *Gnaphosa sericata*, claws IV, apical. **B.** *Eilica* sp., proclaw II, detail of claw–claw tuft clasper. **C.** *Micaria fulgens*, claws I, prolateral-apical. **D.** Same, detail of claw tuft, proclaw and claw–claw tuft clasper.

here denominated metatarsal stopper, which makes contact with a step in the tarsus (fig. 45C). The contact of the stopper triggers the response of the vibration sense organ (Barth, 2002).

TARSUS: The tarsus usually has a dorsobasal step matching the opposing metatarsal stopper. The tarsal organ is situated approximately on the dorsal side of each leg and palpal tarsi, and has hygroreceptor and thermosensory function (see Barth, 2002). The tarsal organ is served by several sensilla with rimmed pores, where the sensory dendrites end. In entelegyne spiders the tarsal organ is protected by a capsule with a small opening (fig. 46B), while in more primitive spiders the sensilla are totally exposed (fig. 47A). The tarsus-pretarsus joint has two condyles, one at each side, allowing movement in the vertical plane (Hill, 1977). Near the condyles there is a pair of slit sensilla, one on each side, sensitive to vibrations (''claw slits,'' Barth and Libera, 1970; ''pretarsal slits,'' Barth, 2002: 80; fig. 45A, B). There may be a ventral unsclerotized suture uniting the claw slits from both sides, the claw-slit suture, which seemingly provides room for cuticle deformation upon stress, and thus increased sensitivity on the slit sensilla (Barth, 2002: chapter VIII, fig. 8). At the tip of the tarsus there may be a group of tenent setae at each side of the claws, the claw tufts, which may arise from well delimited, articulated plates (fig. 45B).

PRETARSUS: The pretarsus is composed by a claw lever and the tarsal claws; it lacks setae. The median or inferior claw is solidly fused with the claw lever (fig. 45A), and is lost in two-clawed spiders (fig. 45B). The paired superior claws articulate with the claw lever and the tarsal tip through a movable membrane. Two tendons control the movement of the claw lever, the pretarsal levator (dorsally), and the pretarsal depressor (ventrally) (Hill, 1977). The claw lever usually has a series of longitudinal ridges at each side, the claw lever file.

CLAWS: The claws are usually pectinate, that is, have a ventral line of teeth foming a comb (fig. 45A). The paired superior claws are normally larger than the median inferior claw.

97. Leg orientation: 0. Prograde (fig. 47A). 1. Laterigrade (fig. 44A). COMMENTS: *Oxyopes*, *Lauricius*, *Borboropactus*, *Geraesta*: Intermediate (scored 01). *Cycloctenus*: contra Homann (1968) (scored 0).

98. Male leg I length: 0. Similar to the rest, or moderately longer (fig. 47E). 1. Much longer than the rest (fig. 47D). The males of several genera of Eutichuridae have extremely long forelegs, sometimes reminiscent of the sensory legs of Amblipygi. COMMENTS: *Hypochilus*: both sexes very long (scored 0). *Cheiracanthium*: long, but not extremely so, male tarsus I only 1.5 of tarsus II (scored 0). *Cheiramiona*: femur I reaching midabdomen; leg I long in female (tarsus I twice as long as tarsus II), but not so exaggeratedly as in male (scored 1). *Macerio*: slightly longer than II (scored 0).

99. Leg III orientation: 0. Backward or laterally (fig. 47C). 1. Forward, here only *Ariadna* (fig. 47B). The third legs oriented forward is often correlated with living in tubes (see references in Izquierdo and Ramírez, 2008).

100. Tarsal cuticle texture: 0. Fingerprint (fig. 95K). 1. Smooth (figs. 95N, 96F). 2. Discrete cells adjacent (fig. 44G) or imbricate (figs. 58F, 89A, 96M). The imbricate or squamate cuticle is a classic character for araneoids (Lehtinen, 1975, 1996). A few intermediate or variable scorings were reported by Griswold et al. (2005: char. 10), and some more are reported here. *Huttonia* has a diffusely imbricate cuticle (fig. 94E). *Galianoella* has imbricate cuticle on tibiae (fig. 96J), but smooth on tarsi. Some terminals have a patchy distribution of fingerprint and smooth cuticle (fig. 94L), or with widely spaced ridges (fig. 96G). Schütt (2003: 145, char. 46) scored a few araneoid terminals as fingerprint, but from observations of the abdominal cuticle, which is differently structured. COMMENTS: *Hypochilus*: from Forster et al. (1987: fig. 17) (scored 0). *Thaida*: from Forster et al. (1987: figs. 99, 100) (scored 0). *Stegodyphus*, *Uloborus*: from Griswold et al. (2005) (scored 1). *Huttonia*: diffusely imbricate (fig. 94E) (scored 2). *Megadictyna*: from Griswold et al. (2005), intermediate, small depressions (scored 01). *Titanoeca*, *Dictyna*: from Griswold et al. (2005) (scored 0). *Neoramia*, *Metaltella*: from Griswold et al. (2005), ambiguous (scored 01). *Pimus*: weak ridges (scored 01). *Macrobunus*: some ridged areas (scored 01). *Aglaoctenus*: see also *Aglaoctenus* sp. in Santos and Brescovit (2001) (scored 0). Cf. *Medmassa* THA: smooth or papillate (scored 1). *Procopius*: slightly papillate in zones (scored 1). *Mandaneta*: sometimes papillate (scored 1). *Olbus*: slightly papillate (Ramírez et al., 2001) (scored 1). *Phrurolithus*: widely spaced ridges, not fingerprint (scored 1). *Camillina*: intermediate (scored 01). *Galianoella*: imbricate on tibia, smooth on tarsi (scored 1). *Legendrena*: mostly smooth, but weak fingerprint on some patches (fig. 96I) (scored 01). *Doliomalus*: weak fingerprint in sectors, otherwise smooth (scored 01). *Platyoides*: there are shallow depressions delimiting cells, similar as in imbricate cuticle (scored 1). *Trachycosmus, Fissarena, Cheiracanthium*: weak but definite ridges (scored 0). *Cithaeron*: bumps and scales (see also metatarsus), also cracks (figs. 55C, 96N) (scored 2). *Uliodon*: tarsal tip smooth (scored 01). *Polybetes*: some areas about smooth (scored 0). *Philodromus*: rugged (scored 1). *Epidius*: very weak fingerprints (scored 01). *Geraesta*: also with bumps (scored 1). *Boliscus*: smooth with many papillate surfaces (scored 1). *Tmarus*: irregular texture (scored 1). *Lyssomanes*: intermediate, perhaps papillate (scored 01).

101. Tarsal cuticle discrete cells disposition: 0. Adjacent (fig. 44G). 1. Imbricate, distal cell margin elevated (figs. 89A, 96M).

102. Retrocoxal hymen: 0. Absent. 1. Present on leg I (figs. 3A, 49A–D). 2. Present on legs I–II. 3. Present on legs I–III. States are ordered. This is an unsclerotized, often elevated patch, on the retrolateral surface of the coxa, found by Robert Raven (see Bosselaers and Jocqué, 2002: 244). Bosselaers and Jocqué scored this character independently for males and females (2002: chars. 1, 2). Here I recorded separately both sexes, and concluded that males and females vary coordinately; the character may occasionally be intraspecifically variable, which may explain the discrepancies with their observations. A few scattered terminals have a hymen also on legs II (Sparianthinae VEN) and III (*Xysticus*). COMMENTS: *Acanthoctenus*, *Ctenus*, *Cycloctenus*: wide unsclerotized patch (scored 1). *Elaver*: only seen in the couple INBio loc. 3339, and very faint (scored 1). *Paccius*: sclerotized (scored 1). *Mandaneta*: very large (scored 1). *Neato*: hard to see, the specimen is weakly sclerotized (scored 1). Miturgidae QLD: among the specimens examined, absent in several males, present in one female (scored 01). *Miturga gilva*: weak, weaker on male (scored 1). *Syspira*: Variable, more often absent. The white area is at the end of an increasing vertical series of setae (scored 01). *Lauricius*: some specimens with a tiny relict (scored 01). *Liocranum*: contra Bosselaers and Jocqué (2002) (scored 1).

103. Retrocoxal hymen size: 0. Small to medium-sized mound (fig. 49D). 1. Large unsclerotized patch. COMMENTS: *Paradiestus*: larger in female (scored 0). Cf. *Medmassa* THA: well elevated (scored 0). *Boliscus*: the one on leg I much larger (scored 1).

104. Leg autospasy location: 0. Between trochanter and coxa. 1. Between patella and tibia. 2. Absent. Most of the scorings are inferred from preserved specimens, when legs are broken consistently at the same articulation. The generalized state (coxa-trochanter) was scored even when only one leg was found broken there. See character 109 for the male tibial crack.

105. Trochanter distal ventral margin: 0. Deeply notched, at least on legs I and II (fig. 47G). 1. Convex, straight, or shallowly notched (fig. 47H).

106. Trochanter IV length: 0. Less than 1.5 times the length of trochanter III. 1. 1.5 times as long as trochanter III or longer (figs. 43F, 47F, 48I).

107. Patellar indentation I–II: 0. Present (fig. 50B). 1. Absent (fig. 50G). In this dataset only *Vectius* lacks the patellar indentation, and in *Platyoides* it is reduced to a great extent. Both are extremely flat spiders with laterigrade legs, and the loss of the indentation seems related with the loss of (morphologically) lateral movements in the patella-tibia joint. Ventral to the lyriform organ there usually is one or more erect setae (fig. 50B–D) (Tharina Bird, in litt., observed in *Ammoxenus*). The lyriform organ is usually placed near the middle of the patella (fig. 50B, D), but a few basal representatives in this dataset have the lyriform organ of legs I and II placed near the distal margin of the patella (fig. 49E, G). In some of those terminals, there is an incision proximal to the lyriform organ (compare fig. 49F, G, with incision, and fig. 49E, without). Such an incision occurs in palpimanids, stenochilids, and *Huttonia*, adding support to the close relationships of those taxa. In the usual conformation with the lyriform organ placed near the middle of the patella, there may be some proximal sutures of diffuse limits. COMMENTS: *Eriauchenius*: lyriform organ on anterior margin on leg I, indentation present on II–IV (scored 0). *Platyoides*: present on legs III and IV, on I and II distally closed, only a small narrow patch distal to a basal lyriform organ (fig. 50E, F) (scored 01). *Vectius*: totally closed in all legs (fig. 50G) (scored 1).

108. Patellar indentation I–II width: 0. Wide (fig. 50A). 1. Narrow (fig. 50B). This character is modified from Bosselaers and Jocqué (2002: char. 6). They described the structure as "a slit-like membranous indentation on the [retrolateral] side of the [patella]. May be very narrow or rather wide." There are many intermediate conditions, scored (01). The indentation is frequently wider on the posterior legs. COMMENTS: *Huttonia*: almost closed, lyriform organ marginal, distal to the indentation (scored 1). *Eriauchenius:* lyriform organ marginal on leg I, wide indentation on the rest (scored 0). *Storenomorpha*, *Oxyopes*, *Apostenus*, *Phrurotimpus*, *Otacilia*, *Orthobula*, Trachelidae ARG, *Gayenna*, *Cheiramiona*, *Strotarchus*, *Ciniflella* BRA, *Tengella*: intermediate (scored 01). *Vectius*: totally closed in all legs, lyriform organ in basal third (scored -). *Platyoides*: narrow on legs III and IV, but on legs I and II distally closed, only a small narrow patch distal to a basal lyriform organ (scored 1). *Oedignatha*: distally narrow (scored 01). *Malenella*: very widely open (scored 0). *Cheiracanthium*: not very narrow (scored 1). *Lauricius*, *Plexippus*: narrow on all legs (scored 1). *Boliscus*: narrow on leg I, very short on leg IV (scored 1).

109. Male tibial crack: 0. Absent. 1. Present, a suture line at the base of the leg tibiae, just distal to the basal pair of ventral spines (see Griswold, 1993: figs. 3–4; Griswold et al., 2005: char. 23). See character 104 for the patella-tibia autospasy of Filistatidae and Austrochilidae.

110. Calamistrum organization: 0. Linear, calamistrum setae in one or more lines (figs. 46C, 51A, C, E). 1. Oval, calamistrum setae in an irregular patch (fig. 52B, C). Because the presence of a calamistrum is perfectly correlated with the occurrence of a cribellum, the former was not retained as an active character in the analysis. COMMENTS: *Eresus*: one line plus dorsal patch of calamistral setae (scored 01). *Badumna*: also dorsal patch of setae, but not of the calamistrum type (scored 0).

111. Calamistral rows: 0. Two. Only Hypochilidae (fig. 51A). 1. One (fig. 51I). 2. Three. *Filistata* has the calamistral setae in three staggered rows (fig. 51F, G), but the more basal calamistral setae still show the triseriate arrangement found in the basal filistatine *Sahastata* and in the Prithinae (fig. 51E).

112. Calamistrum rows setal arrangement: 0. Rows linear (fig. 51E, I). 1. Rows staggered on cuticular ridge. This state is unique to Filistatinae (fig. 51F) (Gray, 1995; Ramírez and Grismado, 1997).

113. Calamistrum origin: 0. Basal, 1. Median. All state 0 in this dataset. This character was used in Griswold et al. (2005: char. 28): "Calamistrum origins were classified based on the following formula: length from the metatarsus base to calamistrum origin divided by the metatarsus length. A ratio of less than 0.30 was considered basal to subbasal (figs. 143E, 145A). A ratio of greater than 0.30 was considered median origin (figs. 143D, 144A)." COMMENTS: *Stiphidion*: because the calamistrum is long, but it is almost median! (scored 0).

114. Calamistrum setae teeth: 0. Absent (fig. 51H, K). 1. Present (fig. 52A, B).

115. Calamistrum setae teeth lines: 0. One line of teeth (figs. 51D, 52A). 1. Two or more lines (fig. 51B, J). COMMENTS: *Ciniflella* BRA: multiple rows (scored 1). *Ciniflella* ARG: the more ventral setae with larger teeth (scored 1).

116. *Hortipes* sensor on dorsal metatarsus I and II: 0. Absent. 1. Present, an oval depression bordered by setae and two trichobothria (fig. 53F–H). A synapomorphy of *Hortipes* (Bosselaers and Jocqué, 2000). They report of immatures of *H. contubernalis*, "[w]hile running, the two pairs of front legs did not touch the substrate most of the time but were held outstretched in an antennalike fashion" (Bosselaers and Jocqué, 2000: 9). These odd structures seem like a directional air motion sensor, the lateral setae shielding signals from the sides and behind.

117. Metatarsal preening comb: 0. Brush or absent. 1. Distinct comb (fig. 53D, E). Several terminals had intermediate morphology, between a brush and a defined comb (fig. 53A–C). COMMENTS: *Ariadna*: IV, retrolateral (scored 1). *Donuea*: comb made of very particular setae, like the chisel-shaped hairs of Jocqué (1991) (scored 1). *Trachelopachys*: comb plus brush (scored 1). *Pseudocorinna*, *Jacaena*, *Sesieutes*: intermediate (scored 01). *Drassinella*: brush (scored 0). Cf. Liocranidae LIB: group of thick setae, but not defined comb (scored 0). *Teutamus*: brush made of same kind of setae as comb in other terminals (scored 0).

118. Metatarsus ventroapical end extension: 0. Truncate or invaginated (fig. 57H). 1. Extending below tarsus (fig. 54C, F, G). COMMENTS: *Plexippus*: much more evident on posterior tarsi (scored 1).

119. Metatarsal dorsodistal stopper: 0. Present (fig. 55D, G). The distal dorsal tip of the metatarsus extended beyond the lyriform organ, overhanging the tarsal base. 1. Absent (fig. 54A, B). The absence of the stopper seems to occur only in cases where the tarsus-metatarsus joint lacks movement, which in turn is apparently correlated with the metatarsus being shorter than the tarsus, as in symphytognathoids (fig. 54A, B) (see also the relictual stopper in *Boliscus*, fig. 54G, H). COMMENTS: *Mituliodon*: membranous, more prominent on leg IV (scored 0). *Xenoctenus*, *Uliodon*: remarkably whitish, flexible, bright (scored 0). *Boliscus*: relictual, tarsus-metatarsus joint seemingly without much movement (fig. 54H) (scored 0).

120. Metatarsal dorsodistal stopper conformation: 0. Solid, about straight distal border (fig. 55D). 1. Membranous, trilobate (fig. 55H–J). A synapomorphy of Sparassidae, seemingly associated with their ability to overflex the tarsus-metatarsus articulation (see also char. 121). COMMENTS: *Cryptothele*: perhaps not much mobility (scored 0). *Zoropsis*: Bosselaers (2002: 141) cites an apical, soft membranous rim on dorsum (scored 0). *Pseudoctenus*: not well sclerotized, cushionlike (scored 0). *Hovops*: that of leg IV asymmetrical (scored 0).

121. Tarsal dorsobasal step matching metatarsal stopper: 0. Present (fig. 55A, E–G). 1. Absent (fig. 54E). *Lyssomanes* lacks the matching step on the tarsus, which seems to be correlated with their ability to overflex the tarsus-metatarsus articulation, as sparassids do (figs. 54D, 218B). The tarsal surface in contact with the metatarsal stopper usually has regularly spaced files, which may play a role in the sensory mechanism as well. COMMENTS: *Filistata*: scored from *Kukulcania*, a very small stopper, seemingly not much movement (scored 0). *Prodidomus, Neozimiris, Lygromma*: with longitudinal striations (scored 0). *Austrachelas*: a pair of slit sensilla just apical and at sides of step (fig. 55E) (scored 0).

122. Tarsus base sclerotization: 0. Sclerotized. 1. Weakly sclerotized ring. This character has been proposed as a synapomorphy of Archaeidae and Mecysmaucheniidae (Forster and Platnick, 1984: 104). In this matrix, it is present in *Eriauchenius* (Archaeidae), but also in *Desis* (Desidae).

123. Female tarsal cuticle continuity: 0. Entire, not cracked or pseudosegmented (fig. 58D). 1. Cracked or pseudosegmented (figs. 56A, B, 57A–D). COMMENTS: *Psechrus*: flexuose, no clear cracks (scored 0). *Apostenus*: only tarsus IV (scored 01). Cf. Liocranidae LIB: on a median segment of tarsus IV (scored 01). *Meedo*: "At least tarsi III of males (often other tarsi as well, in both sexes) with cuticular cracks at about two-thirds their length" (Platnick, 2002: 23) (scored 1). *Neato*: cracked, irregular sclerotized fields remain (fig. 58A, B) (scored 1). *Cithaeron*: cracks not completing rings (fig. 57D) (scored 1). *Ammoxenus*: some of the cracks completing rings (fig. 57B) (scored 1).

124. Female tarsi curvature: 0. Straight (fig. 56E). 1. Slightly bent (fig. 56G). 2. Strongly bent to coiled (figs. 56A, 57A, C). States are ordered. COMMENTS: *Senoculus*: straight (scored 0). *Pseudoctenus*: only slightly bent in female, because the tarsi are short (scored 0). *Apostenus,* cf. Liocranidae LIB: only IV bent (scored 0).

125. Male tarsus IV curvature and cuticle: 0. Straight or with continuous cuticle. 1.

Bent, pseudosegmented. This is a modification of character 9 in Bosselaers and Jocqué (2002). COMMENTS: *Cycloctenus*, *Toxopsiella*: curved, not pseudosegmented (scored 0). *Agroeca*: pseudosegmented (scored 1). *Apostenus, Ammoxenus*: male and female (scored 1). *Cithaeron*: all tarsi bent (scored 1). Cf. Liocranidae LIB: same as female (scored 1). *Teutamus*: a cracked area on the distal 1/5 (scored 1).

126. Tarsal organ conformation: 0. Exposed. The nerve endings are visible on the cuticle (fig. 47A). 1. Capsulate. The nerve endings are placed inside a cuticular pocket, accessible to the outside through a hole (fig. 58I, J). COMMENTS: *Hypochilus*: from Forster et al. (1987: fig. 17) (scored 0). *Thaida*: from Forster et al. (1987: figs. 99, 100) (scored 0). *Ariadna*, *Stegodyphus*, *Uloborus*, *Megadictyna*, *Titanoeca*, *Dictyna*: from Griswold et al. (2005: figs. 151–153). *Corinna*: see also Bonaldo (2000: fig. 67). *Creugas, Micaria, Ammoxenus, Anyphops*: not found (scored ?). *Xenoplectus*: from female palp (scored 1). *Gayenna*: from leg IV (scored 1). *Amaurobioides*: badly resolved in SEM but visible (scored 1). *Liocranoides*: from Platnick (1999: fig. 1) (scored 1).

127. Tarsal organ opening shape: 0. Round to oval (fig. 58L–N). 1. Teardrop or keyhole. The posterior margin of the opening is constricted (fig. 58G, K). Several terminals have limiting shapes, similar to oval (fig. 58I). 2. Long slit. The opening is very elongated in a long slit (fig. 58H). 3. Stellate. Only in *Griswoldia* in this dataset, this state was discovered by Griswold (1993: char. 56, state 2). *Meriola* is somewhat intermediate between oval and slit (fig. 58O). COMMENTS: *Uloborus*, *Megadictyna*, *Titanoeca*, *Dictyna*: from Griswold et al. (2005: figs. 151–153). *Pimus*: from *Pimus napa* (fig. 58G), but a *Pimus* indet. from Mendocino Co., California, has a round opening (Griswold et al., 2005: fig. 153J) (scored 1). *Zoropsis*: not markedly so (fig. 58I; see also Griswold, 1993: fig. 66) (scored 1). *Toxopsiella*: very long slit (fig. 58H) (scored 2). *Clubiona*: intermediate (scored 01). *Elaver*: most clear in leg IV (scored 1). *Donuea*: I teardrop, IV and palp oval (scored 01). *Griswoldia*: from *Griswoldia acaenata*, but teardrop on female palp (Griswold, personal commun.) (scored 3). *Meriola*: intermediate between oval and slit (scored 02). *Orthobula*: too dirty to see (scored ?).

128. Leg tarsal organ turret: 0. Absent. The tarsal organ is superficial (figs. 47A, 58M). 1. Present. The tarsal organ is placed at the top of a turret (fig. 68B; Griswold, 1991: fig. 29). Raven and Stumkat (2005: char. 50, state 3) report a similar structure in the zoropsid genera *Megateg*, *Krukt*, and *Birrana.* COMMENTS: *Griswoldia*: from *G. acaenata*, but absent in other species (Griswold, 1991) (scored 1). Sparianthinae VEN: the tarsal organ is superficial on the female palp (scored 1). *Boliscus*: just slightly protruding (scored 0).

129. Tarsal sensory field depression: 0. Absent. The region bearing the trichobothria and tarsal organ at the same level as the rest of the tarsus (fig. 58C). 1. Present. The trichobothria and tarsal organ are grouped in a common apical depression (fig. 95A). Present only in *Borboropactus* in this dataset. This was called "tarsal pit organ" by Wunderlich (2004: 1738), one of the characters defining his "Borboropactidae" (see Thomisidae).

130. Apical ventral tarsal cuticle sclerotization: 0. Entire, sclerotized (fig. 73A). 1. Unsclerotized transverse suture below claws (figs. 45A, 59E, 60F, 61A, 62B, 68E, H, 69E, 75E, 76B). The suture seems always associated to the pair of ventral apical slit sensilla ("claw slits," figs. 45A, 60D, 76B), thus it is called here *claw-slit suture*. In sparassids other than sparianthines, the claw-slit suture is served by four or more slit sensilla along the suture (fig. 68E, H). COMMENTS: *Dolomedes*: only a depressed area in SEM (scored 0). *Acanthoctenus*: tenuous (scored 01). *Senoculus*: a well-defined articulation separated from claws (scored 1). *Castianeira*: there is a thin flexible line continued from the slit sensilla (fig. 69E) (scored 1). *Ammoxenus*: all pseudosegmented (scored -). *Selenops*: leaving a tight bunch of setae below claw tufts (scored 1). Sparianthinae VEN: wide membranous area leaving the most apical ventral setae apart (scored 1).

131. Extent of claw-slit suture: 0. Partial division, ventral, not reaching anterior superior margin (figs. 59E, 61A, F). 1. Total division, suture reaching anterior or superior margin (figs. 68E, 75E). COMMENTS: *Uloborus, Mimetus*: tarsus IV, suture not a complete ring, interrupted in retrolateral dorsal sector (scored 0). *Huttonia*: totally divided on leg IV, almost totally on leg I (scored 01). *Eriauchenius*: suture reaching dorsal margin (fig. 59C) (scored 1). *Stiphidion*: suture reaching anterior dorsal margin (scored 1). *Vulsor*: suture tenuously reaching anterior margin (scored 01). *Phrurolithus*, *Otacilia*, *Drassinella*: suture reaching anterior margin (figs. 75E, 76B–D) (scored 1).

132. Serrate accessory claw setae: 0. Absent. 1. Present (figs. 59A, B, D, 60A). COMMENTS: *Stiphidion*: very weakly serrated (Gray and Smith, 2008: fig. 3k) (scored 0). *Homalonychus*: Two large tenent setae. *Zimiris* (Prodidominae) has similar setae, without a tenent surface (Platnick and Penney, 2004: fig. 15) (scored 0). *Oxyopes*: one lateral short seta slightly serrate (fig. 62B) (scored 01). *Senoculus*: only on prolateral side (fig. 60G) (scored 1).

133. Serrate accessory claw setae thickness: 0. Slender, as tactile hairs (figs. 59D, 59B, 60G). 1. Thick, as macrosetae (figs. 59A, F, 60A). Compare the thickness of macroseta and accessory claw setae in figure 59A and B.

134. Inferior tarsal claw I size: 0. Large (fig. 60D). 1. Small (fig. 60C). 2. Absent (fig. 65C). States are ordered. "Genera as *Griswoldia*, *Phanotea* (Griswold, 1991, 1994), and *Janusia* may have a small ITC on the anterior legs and only nubbins or none on the posterior legs" (Silva Davila, 2003: char. 111). COMMENTS: *Ctenus*: Homann (1971) reports that *Ctenus* first and second instars have an ITC, in part with teeth (scored 12). *Griswoldia*: small claw on legs I–II, reduced to a nubbin in III–IV (scored 1).

135. Inferior tarsal claw teeth: 0. Toothed (fig. 60D). 1. Smooth (fig. 60E). COMMENTS: *Ariadna*: one small tooth (scored 0). *Huttonia*: from Platnick and Forster (1984: fig. 341) (scored 0). *Psechrus*: three teeth in immatures, two in adult (Homann, 1971) (scored 0).

136. Inferior tarsal claw symmetry: 0. Nearly symmetric. 1. Strongly asymmetric (figs. 59A, 60B, G). COMMENTS: *Thaida*: claw I curved toward prolateral side, IV toward retrolateral (scored 1). *Araneus*: claws rotated about 45°, I–II to prolateral, III–IV to retrolateral (scored 1). *Megadictyna*: Griswold et al. (2005: fig. 137B) is ambiguous for this (scored ?). *Senoculus*: curved to prolateral side, on all legs (scored 1).

137. Inferior tarsal claw IV curvature: 0. Dorsally convex or approximately straight (fig. 60D, E). 1. Sigmoid, dorsally concave reaching the tip (figs. 59F, 60A). The elongate, sigmoid inferior tarsal claws are characteristic of some symphytognathoids (Coddington, 1986; Griswold et al., 1998; Schütt, 2003). COMMENTS: *Thaida*: claw IV, slightly sigmoid (scored 01). *Dictyna*: claw broken in preparation (scored ?). *Mimetus*: very slightly sigmoid (scored 01). *Dictyna*: claw broken (scored ?).

138. Superior tarsal claws teeth: 0. Toothed (fig. 60D). 1. Smooth (figs. 61B, 79D, 82B). Bosselaers and Jocqué (2000: char. 64) scored leg IV. COMMENTS: *Prodidomus*: claws very long, some distal markings might be relics of teeth (fig. 82B) (scored 1). *Neozimiris, Selenops, Hovops*: intermediate, relictual teeth (fig. 62E) (scored 01). *Phrurolithus*: one blunt tooth on retroclaw I (fig. 75E) (scored 01).

139. Superior tarsal claws I teeth symmetry: 0. Both claws similarly toothed (figs. 70F, 79C, E). 1. Retroclaw with many fewer teeth than proclaw (figs. 64D, G, 65B, 66D, 67D, E). COMMENTS: *Zoropsis*: male with more teeth (Homann, 1971) (scored 1). *Philodromus*: also noted and discussed by Homann (1975) (scored 1). *Borboropactus*: counting the lateral comb, which in other stephanopines is more integrated into normal teeth (scored 2). *Holcolaetis*: retroclaw smooth (scored 1). *Falconina*: two teeth each claw on I, one each on IV (scored 0). Cf. Liocranidae LIB: claws I with more, longer teeth than IV (scored 0). *Vectius*: I proclaw 8, retroclaw 6; IV proclaw 6, retroclaw 4 (scored 0). *Anyphaena*: proclaw ca. 17, retroclaw 7 (scored 1). *Odo bruchi*: almost identical side by side (scored 0). *Stephanopoides*: proclaw ca. 16 with several small basals, retroclaw 10 (fig. 64D) (scored 1). *Boliscus*: proclaw 10, retroclaw 12 (scored 0). *Thomisus*: proclaw 13, retroclaw 7 (scored 1).

140. Proclaw external comb in defined patch: 0. Absent (fig. 70F) or not well defined (fig. 64F). 1. Well defined patch of teeth forming a comb (fig. 64A). This occurs in *Borboropactus* in this dataset, it was also observed in other stephanopine thomisids.

141. Superior tarsal claw teeth insertion line: 0. Ectal line (figs. 64F, 67C, 79F). 1. Median line (fig. 79G). 2. Mesal line (figs. 64H, 71C, 77A, 78A, B, 79C). States are ordered. This is a modification of classic character of zodariids (Jocqué, 1991: char. 3). Several terminals have oblique (fig. 62D) or sinuous (fig. 60G) lines of teeth and were scored ambiguous. COMMENTS: *Eresus*: basal ectal, apical mesal (scored 012). *Nicodamus*: not markedly so (scored 2). *Cyrioctea*: teeth insertion may be slightly mesal (scored 1). *Cybaeodamus*: teeth insertion slightly sinuous, basally median (scored 2). *Cryptothele*: teeth mesal, but reduced on leg IV (scored 2). *Storenomorpha*: retroclaw mesal, proclaw sinuous, basal ectal apical mesal (scored 2). *Acanthoctenus*, *Ctenus*, *Vulsor*, *Liocranoides*, *Lyssomanes*: oblique line, basals slightly ectal (scored 01). *Elaver*: claw thickness interferes a little (scored 01). *Liocranum*: slightly ectal (scored 01). *Otacilia*: reduced teeth, oblique line basals slightly ectal (scored 012). *Galianoella*: slightly ectal (scored 01). *Ciniflella* BRA: only slightly ectal (scored 01). *Pseudolampona*: very slightly internal, scored as median (scored 1). *Borboropactus*: ectal all legs, also in *Onoculus* and *Epicadus* (scored 0). *Strophius*: sinuous, basally slightly external (fig. 64H) (scored 2). *Hispo*, *Plexippus*: proclaw ectal (fig. 67D) (scored 0).

SETAE

A seta is a cuticular outgrowth articulated in a socket through an unsclerotized membrane. A small portion of leg cuticle may have many types of setae (fig. 84A). Setae are most often innervated as a mechanical or chemical sensillium; so far the only setae known to lack innervation seem to be the scales and some scopular setae (Foelix, 2011: 85; Townsend and Felgenhauer, 1999). Table 4 summarizes the external characteristics of the more generalized morphological types of setae. Other specialized setae of more restricted distribution (e.g., those of cheliceral margins, endites, coxal setal pads) are treated separately according to the structures where they occur. There may be, however, other setae types of generalized distribution and unremarkable morphology that remain to be diagnosed.

TACTILE HAIR: The tactile hairs, usually referred simply as "hairs," are the most frequent and widespread kind of setae. They are medium sized, have a curved shaft so that the tip is inclined toward the cuticle, and usually have barbs (fig. 84A). They are innervated by three neurons.

MACROSETA: Also known as spines, macrosetae are large articulate setae, with a thick and long shaft and robust socket (fig. 84B). Macrosetae are innervated by three neurons and become erect when the hemolymph pressure increases. Nerve impulses are generated only during the erection phase. They occur mainly on appendages, but sometimes similar setae occur on the abdomen or cephalothorax as well. The leg macrosetae occur in stereotyped patterns on the legs of spiders of the RTA clade, thus there are more or less standardized nomenclatures to describe the occurrence of macrosetae at given positions (e.g., Ramírez, 2003: 7, 51).

SCALE: Scales are setae with a small socket, bent in angle immediately after the insertion, so that they lay parallel to the cuticular surface (fig. 84C; Hill, 1979; Townsend and Felgenhauer, 1998a, 1998b, 1999; Townsend and Felgenhauer, 2001). As far as we know, scales lack innervation (Townsend and Felgenhauer, 1999). They may occur in a wide diversity of shapes.

TENENT SETA: The claw tufts (fig. 85C) and scopulae (fig. 85D) are composed of setae specialized in adhesion to smooth surfaces. They have a defined patch of barbs with expanded tips, which make contact with the substratum and produce adherence through molecular forces. The same adhesion mechanism is used by hairs and pads of many animals, from beetles to lizards (Arzt, 2003).

PSEUDOTENENT SETAE: These are setae with intermediate morphology between tenent and tactile hair, with acute tip and tenent barbs loosely organized on the contact side but usually not forming a pad (fig. 85E).

TRICHOBOTHRIA: The trichobothria (fig. 84D) are sensory setae on the dorsal surfaces of legs and palps, specialized in detecting air movement (see Barth, 2002). The setal shaft is slender, perpendicular to the cuticle surface, usually curved backward and longer than the neighboring setae. They are disposed

TABLE 4

Characteristics of main types of setae

Seta	Socket	Innervation	Shaft	Shaft angle relative to cuticle	Shaft barbs	Distribution	Stereotyped patterns
Tactile hair	Simple	Triple		Narrow angle, tip curved down	Tapering	All	No
Macroseta	Large	Triple	Thick, rigid	Parallel to orthogonal, movable	Tapering	Appendages prosoma, occasionally abdomen	Stereotyped in RTA clade
Scale	Small	No	Slender or flat, diversity of shapes	Basal angle, parallel	Diversity of shapes	All	No
Tenent (scopular)	Often simple, sometimes indented	Usually none	Wide or truncate tip, tenent pad on contact side	Narrow angle	Tenent barbs with expanded tips forming pad, tapering barbs elsewhere	Legs (palp), mostly ventral	Loose
Tenent (claw tuft seta)	Often simple, grouped in pads, diversity of shapes	?	Wide or truncate tip, tenent pad on contact side, diversity of shapes	About orthogonal to insertion pad, diversity of shapes	Tenent barbs with expanded tips forming pad, tapering barbs elsewhere	Legs (palp), apical	Loose
Pseudotenent	Simple	?	Acute tip. Tenent barbs on contact side, usually not organized in a definite pad	Narrow angle (on leg articles) or orthogonal (near claws)	Tenent barbs with expanded tips on contact area, tapering barbs elsewhere	Legs (palp), apical or ventral	Loose
Trichobothria	Hollow capsule, two plates	Triple	Long, slender, basal expansion, curved backwards	About orthogonal	Tapering	Legs, palp, mostly dorsal	Yes, growing series.
Chemosensory	Small, articulation membrane more exposed than in tactile hairs	Usually 2 mechanical + 19 chemosensory	Apical pore, often whorled sector	Wide angle, sigmoid, tip curved up	Tapering, often reduced or absent	Legs, palp	No

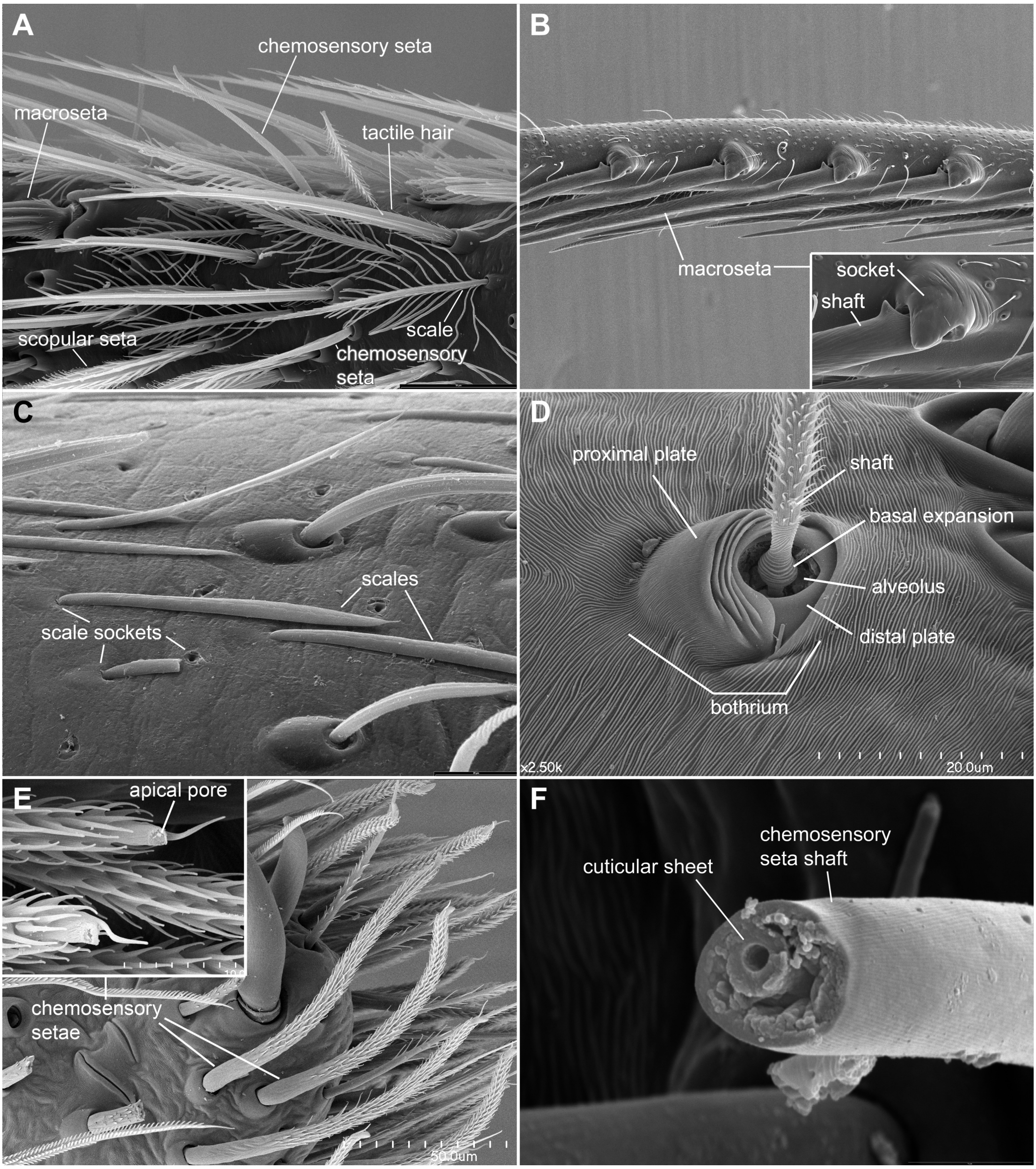

A
chemosensory seta
macroseta
tactile hair
scopular seta
scale
chemosensory
seta
B
macroseta
socket
shaft
C
scales
scale sockets
D
proximal plate
shaft
basal expansion
alveolus
distal plate
bothrium
x2.50k
20.0um
E
apical pore
chemosensory
setae
50.0um
F
chemosensory
seta shaft
cuticular sheet

Fig. 84. Types of setae. **A.** *Titanebo mexicanus* (Philodromidae) female, setae on metatarsus I. **B.** *Teutamus* sp. (Liocranidae) female, macrosetae on tibia I. **C.** *Platyoides walteri* (Trochanteriidae) female, scales on tibia I. **D.** Sparianthinae VEN (Sparassidae) female, trichobothria on tarsus. **E.** *Pardosa moesta* (Lycosidae) male, chemosensory setae on tip of cymbium. **F.** *Ariadna boesenbergi* (Segestriidae) female, sectioned chemosensory seta on tip of tarsus.

in longitudinal series of distally increasing length. Just above the thin articulation with the socket there is a basal expansion that may be variously sculptured. The socket forms a cup or bothrium, with an ample central cavity. The opening of the cup (alveolus) restricts the movement of the setal shaft. The bothrium is usally divided in proximal and

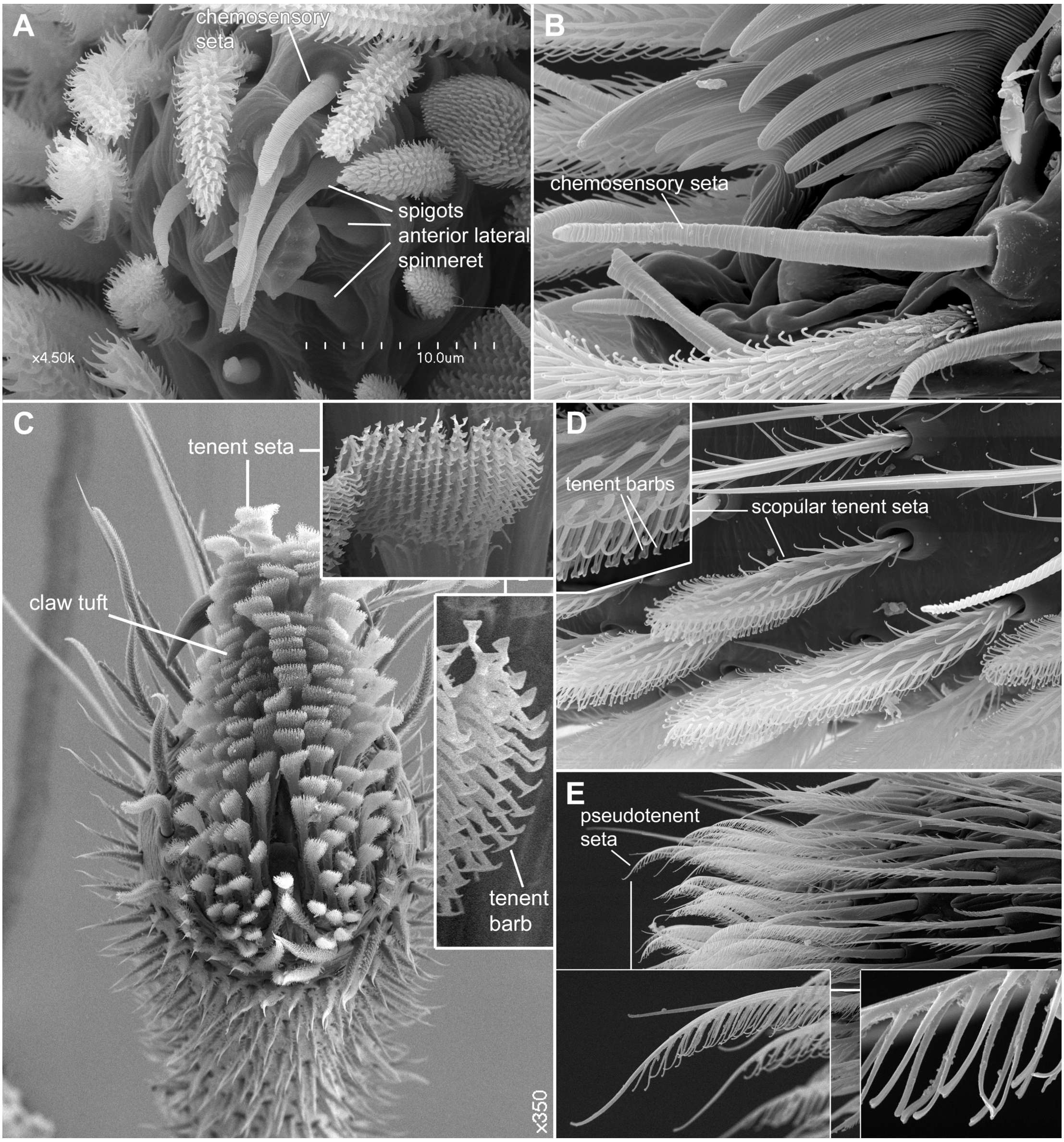

A
chemosensory seta
spigots anterior lateral spinneret
×4.50k
10.0um
B
chemosensory seta
C
tenent seta
claw tuft
tenent barb
x350
D
tenent barbs
scopular tenent seta
E
pseudotenent seta

Fig. 85. Types of setae. **A.** *Misionella mendensis* (Filistatidae), early spiderling, dispersing stage, chemosensory seta on left ALS. **B.** Same, chemosensory seta on tip of tarsus I. **C.** *Donuea* sp. ("Liocranidae"), female, claw tuft on right leg IV. **D.** *Titanebo mexicanus* (Philodromidae), female, scopular setae on tarsus I. **E.** *Stephanopoides brasiliana* (Thomisidae), male, pseudotenent setae on tip of cymbium.

distal plates; the proximal plate is often called trichobothrial "hood."

CHEMOSENSORY SETAE: Sensory setae with an open tip (fig. 84E), chemosensory setae are usually innervated by 21 neurons, two of them mechanosensitive and restricted to the base, and 19 chemosensitive, with their dentrites extending into the shaft, and ending in the distal pore (see Barth, 2002). The shaft has an internal cuticular tube (fig. 84F) enclosing the dentrites, extending from the pore to about 2/3 of the shaft length (Foelix,

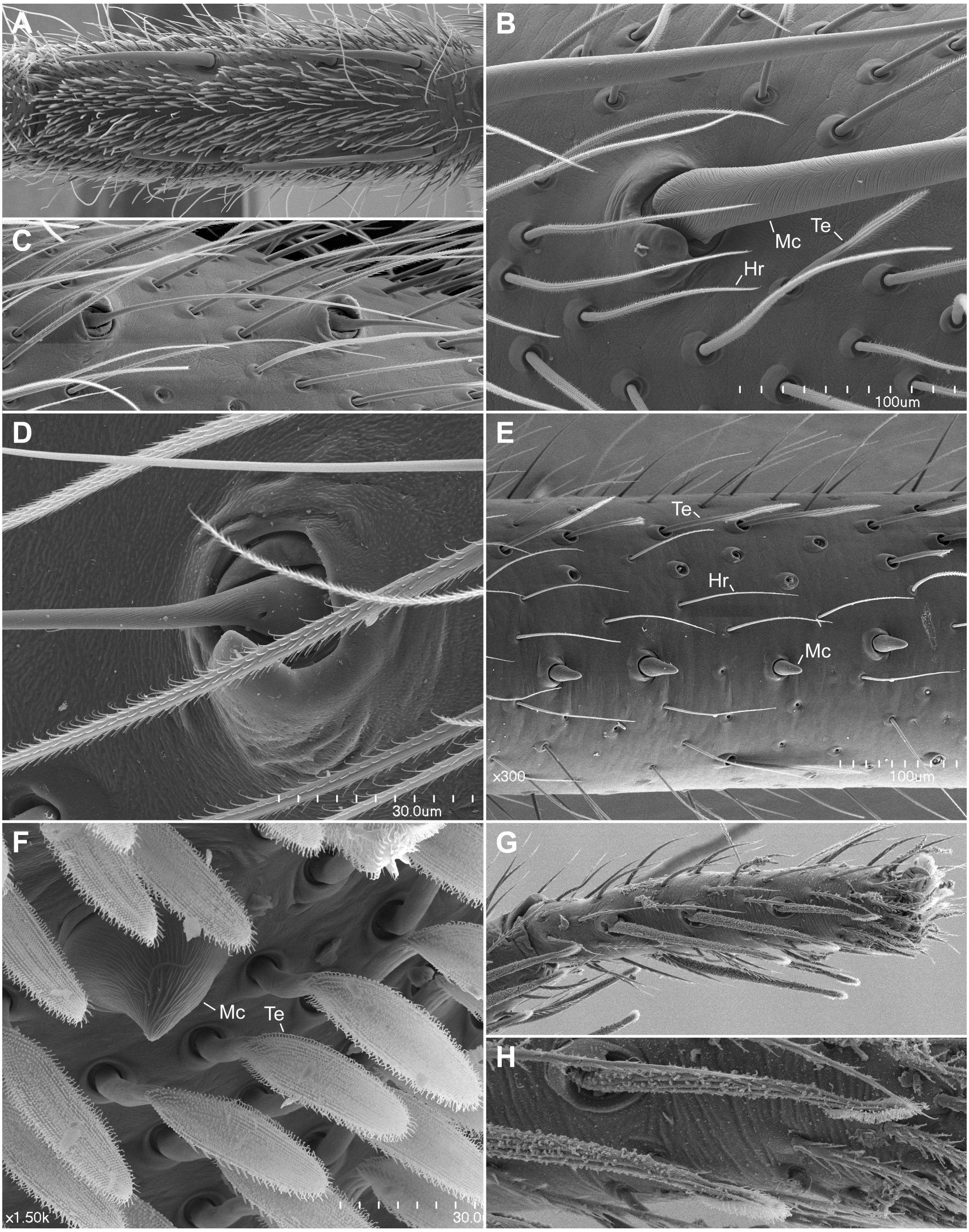


Fig. 86. Leg macrosetae, left side. **A.** *Brachyphaea* cf. *simoni* (Corinnidae), female, metatarsus I ventral, macrosetae and scopula. **B.** Same, tibia I, detail of ventral macroseta. **C.** Same, male, modified ventral macrosetae on tibia I. **D.** Same, detail of macroseta. **E.** *Meriola barrosi* (Trachelidae), male, ventral cusps on tibia I. **F.** *Paccius* cf. *scharffi* (Trachelidae), female, ventral cusp among scopular setae on metatarsus I. **G.** *Orthobula calceata* (Phrurolithidae), female, tarsus I prolateral. **H.** Same, detail of macrosetae with tenent tip.

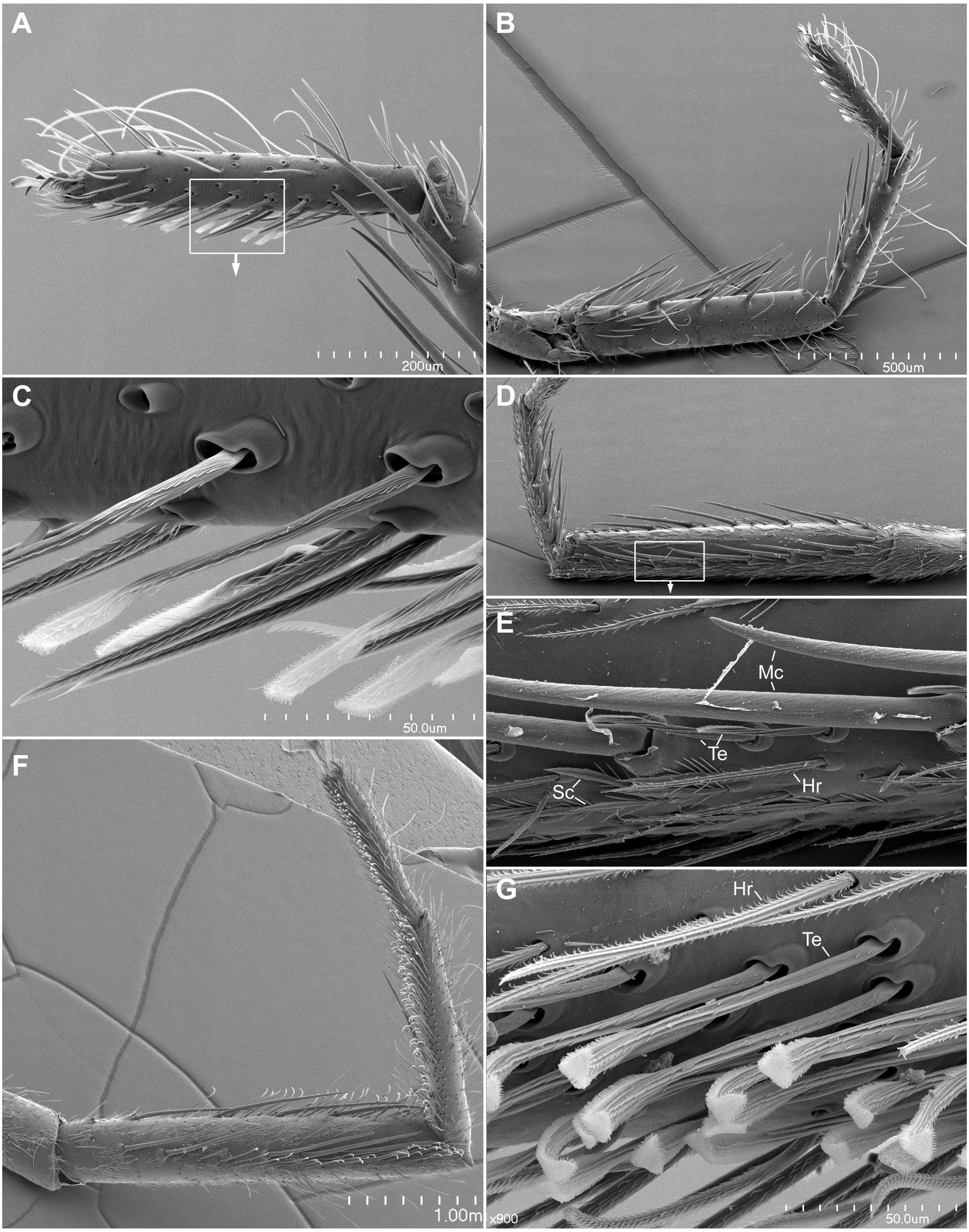


Fig. 87. Leg macrosetae and scopula, female. **A.** *Apostenus californicus* (Liocranidae), left tarsus I, retrolateral, inset enlarged in C. **B.** Same, leg, retrolateral. **C.** Same, detail of tarsal thick scopular setae, retrolateral. **D.** *Drassinella gertschi* (Phrurolithidae), left tibia and metatarsus I, retrolateral-ventral, inset enlarged in E. **E.** Same, detail of macrosetae and scupular setae. **F.** *Liocranum rupicola* (Liocranidae), right leg I, prolateral. **G.** Same, detail of tarsal scopular setae.

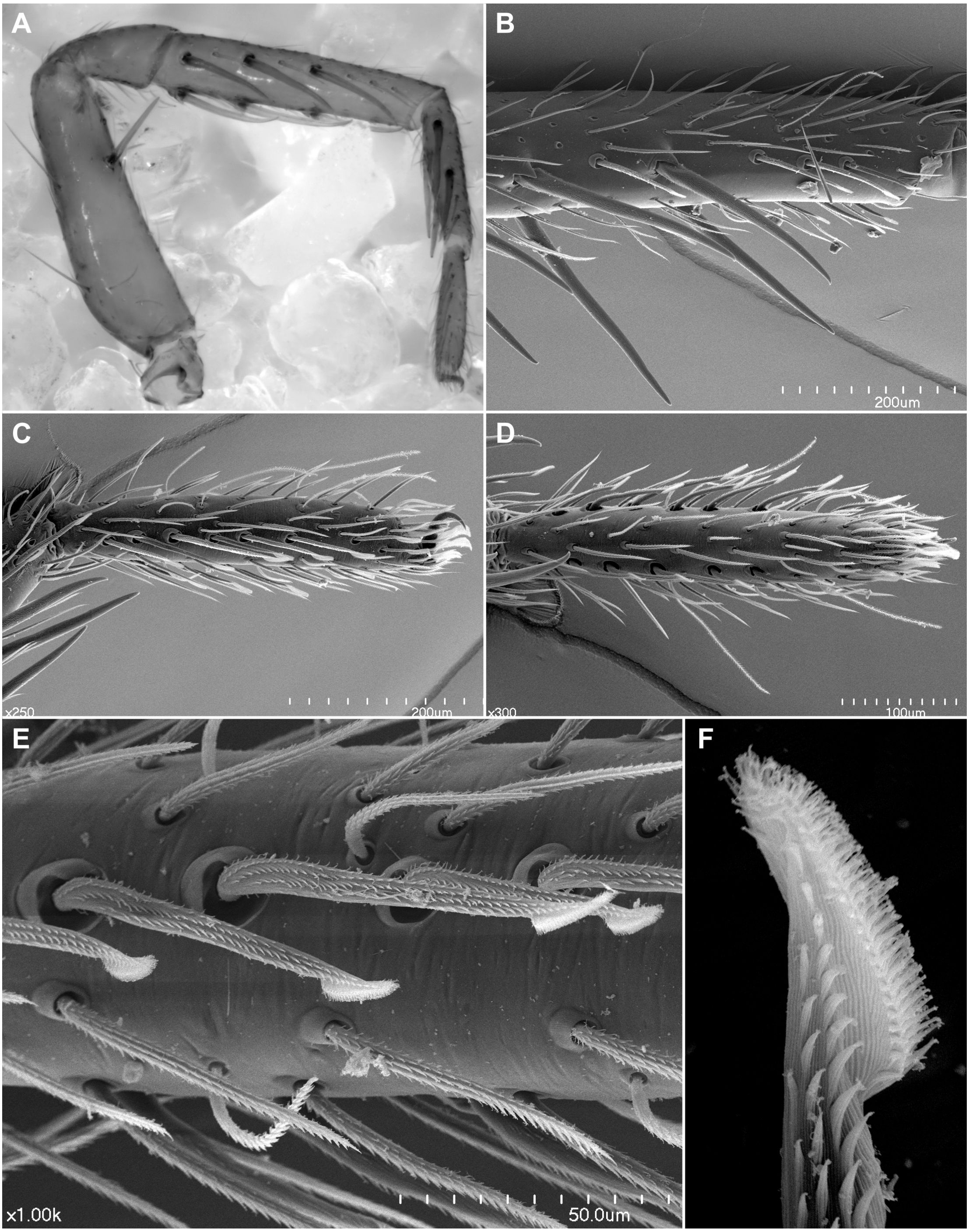

A
B
200um
C
x250
200um
D
x300
100um
E
x1.00k
50.0um
F

Fig. 88. Leg macrosetae and scopula, female of cf. *Moreno* ARG, left leg I. **A.** Leg, prolateral. **B.** Macrosetae on tibia, prolateral. **C.** Tarsus, prolateral. **D.** Same, ventral. **E.** Same, detail of tenent macrosetae. **F.** Same, detail of tenent tip.

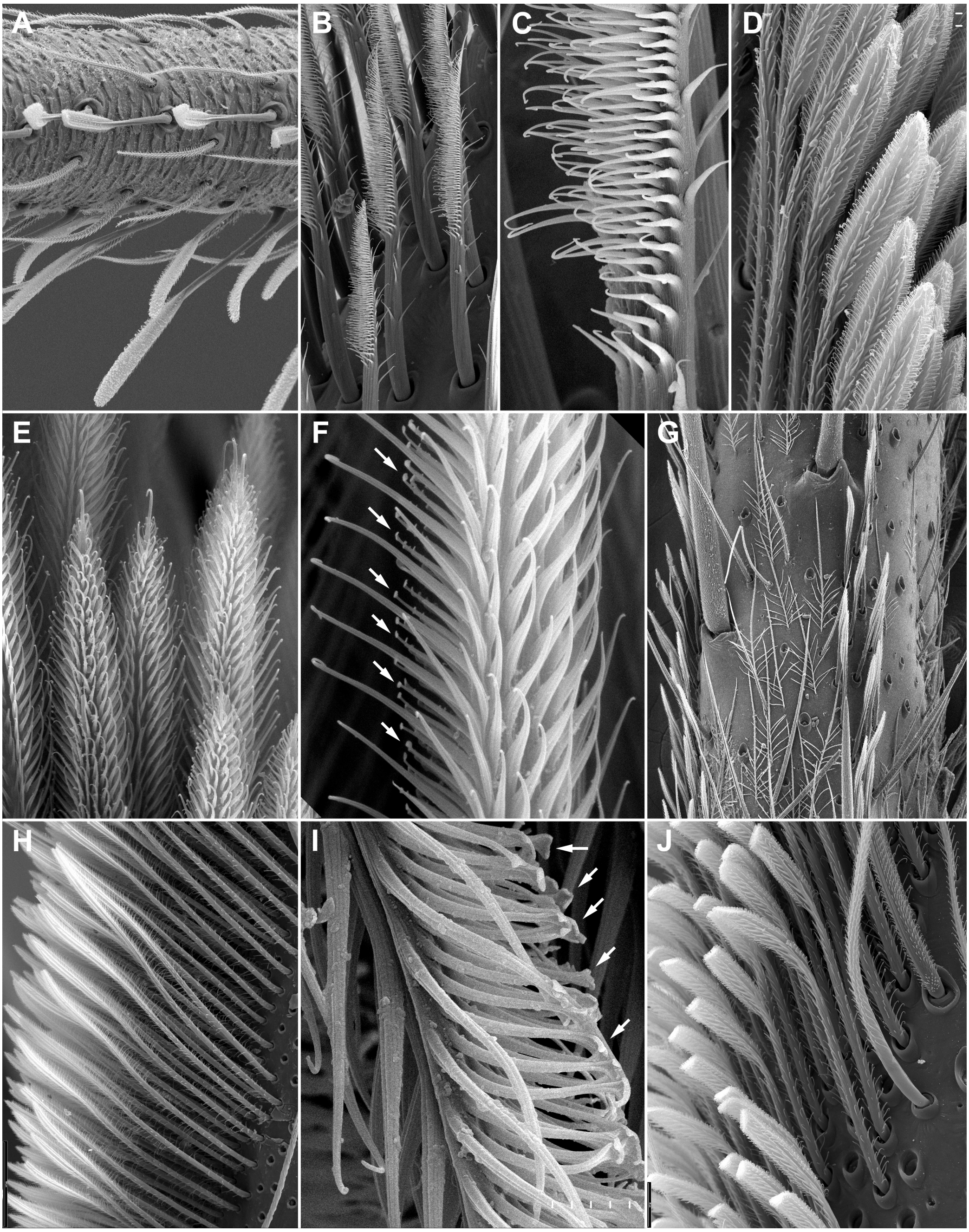


Fig. 89. Scopula and scopular setae, female. **A.** *Eriauchenius workmani* (Archaeidae), tibia I. **B.** *Cybaeodamus taim* (Zodariidae), scopula on tarsus I, with setae similar to pseudotenent seta. **C.** Same, detail of one seta showing acute barbs only. **D.** *Lauricius hooki* (Tengellidae), tarsus I. **E.** *Uliodon* cf. *frenatus* (Zoropsidae), detail of pseudotenent setae on tarsus IV. **F.** Same, detail of one seta, showing tenent barbs (arrows). **G.** *Neoanagraphis chamberlini* ("Liocranidae"), tibia I, ventral. **H.** *Eusparassus* cf. *walckenaeri* (Sparassidae), tarsus I. **I.** *Macerio flavus* (Eutichuridae), detail of tarsal scopular seta, showing tenent barbs (arrows). **J.** *Odo bruchi* (Miturgidae), metatarsus I.

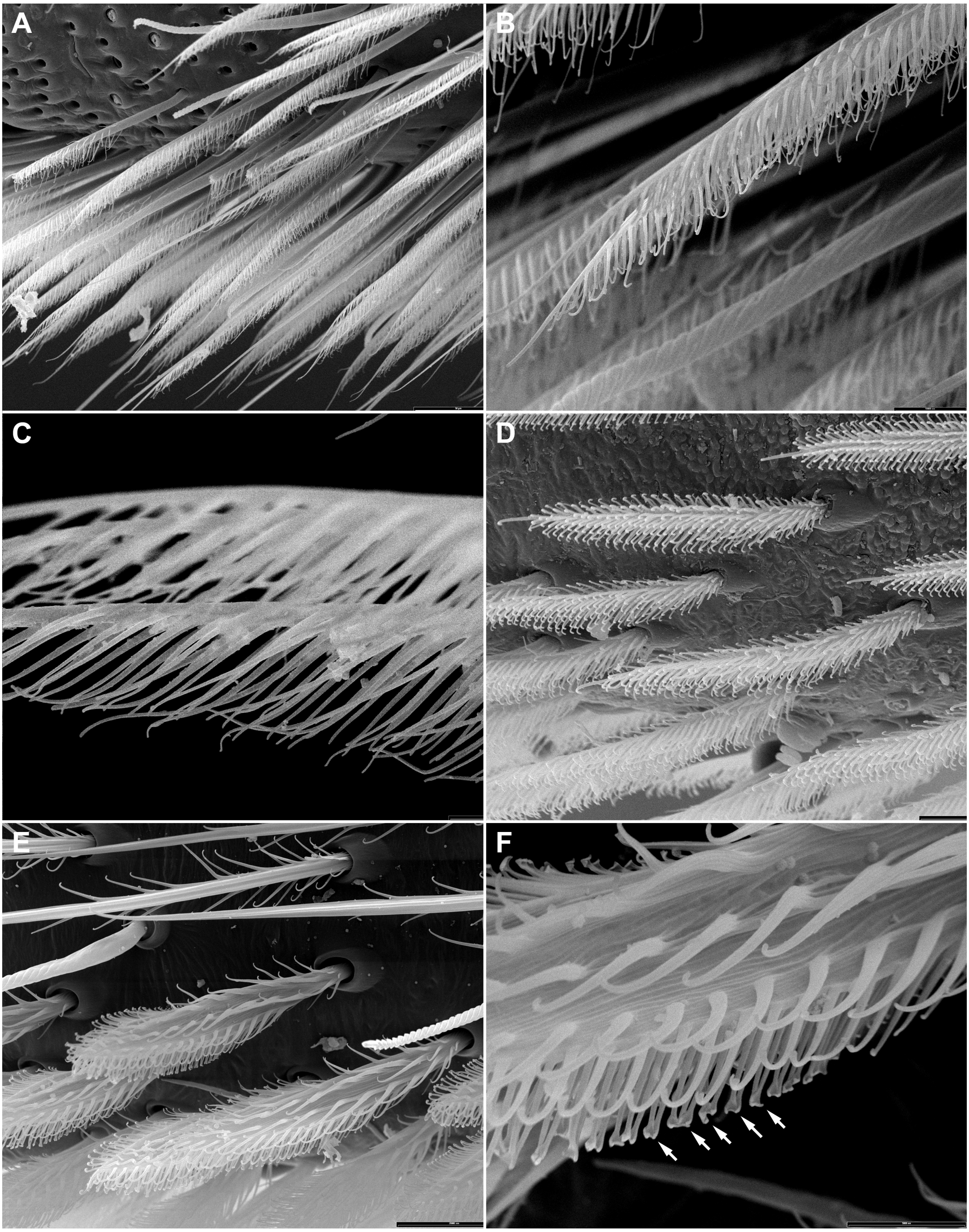


Fig. 90. Scopula and scopular setae, tarsus I. **A.** *Stephanopoides sexmaculata* (Thomisidae), female, scopular setae similar to pseudotenent, but without tenent barbs. **B.** Same, detail. **C.** Same, detail of setal barbs. **D.** *Boliscus* cf. *tuberculatus* (Thomisidae), subadult female, scopular setae without tenent barbs. **E.** *Titanebo mexicanus* (Philodromidae) female, scopular setae. **F.** Same, detail of a scopular seta, showing tenent barbs (arrows).

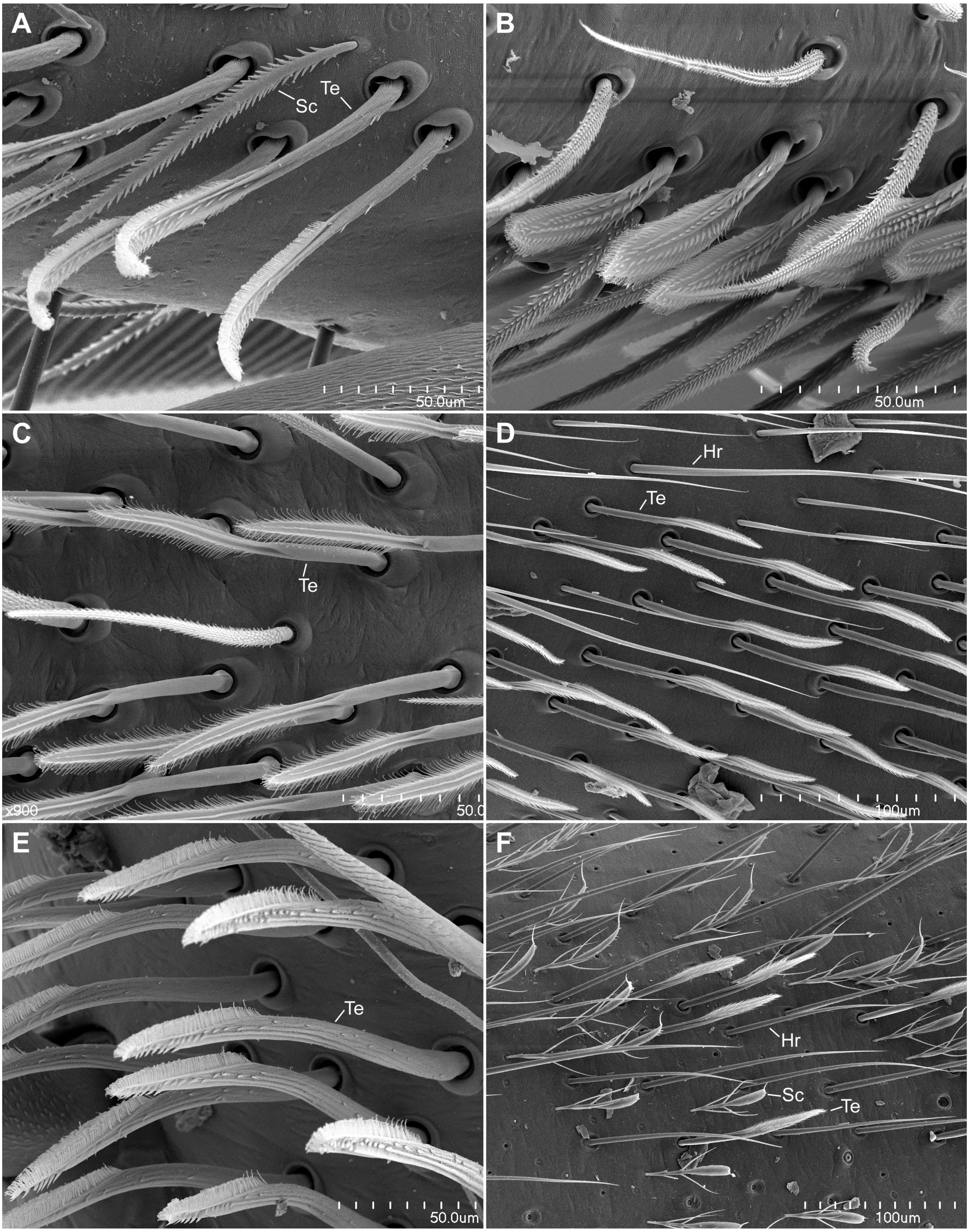

A
Te
Sc
50.0um
B
50.0um
C
Te
x900
50.0
D
Hr
Te
100um
E
Te
50.0um
F
Hr
Sc
Te
100um

Fig. 91. Scopular setae, female. **A.** *Cocalodes longicornis* (Salticidae), tarsus I. **B.** *Portia schultzi* (Salticidae), tarsus I. **C.** *Brachyphaea* cf. *simoni* (Corinnidae), tarsus I. **D.** *Paccius* cf. *scharffi* (Trachelidae), tarsus I. **E.** *Fissarena castanea* (Trochanteriidae), tarsus I. **F.** *Centrothele mutica* (Lamponidae), tarsus I or II.

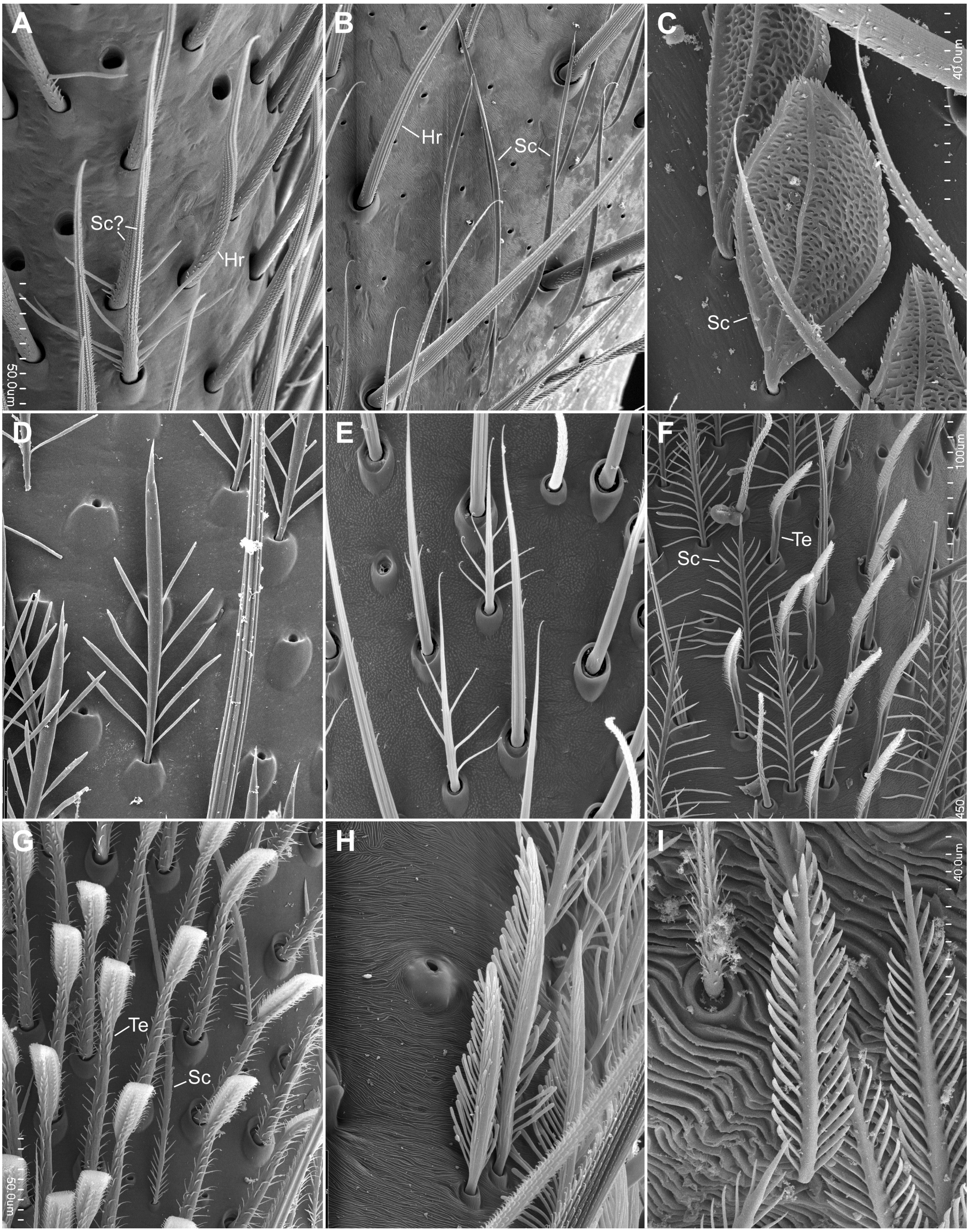

A
Sc?
Hr
50.0um
B
Hr
Sc
C
40.0um
Sc
D
E
F
100um
Te
Sc
450
G
Te
Sc
50.0um
H
I
40.0um

Fig. 92. Scales. **A.** *Thaida peculiaris* (Austrochilidae), female tarsus IV. **B.** *Uliodon* cf. *frenatus* (Zoropsidae), female tibia I. **C.** *Oxyopes heterophthalmus* (Oxyopidae), female chelicera. **D.** *Creugas gulosus* (Corinnidae), female tibia I. **E.** Cf. *Medmassa* THA (Corinnidae), subadult female, metatarsus I. *Plexippus paykulli* (Salticidae) female, abdomen. **F.** *Copa flavoplumosa* (Corinnidae), female tibia I. **G.** *Syspira eclectica* (Miturgidae), female tibia I. **H.** *Quemedice enigmaticus* (Sparassidae), male tarsus IV. **I.** *Plexippus paykulli* (Salticidae), female abdomen.

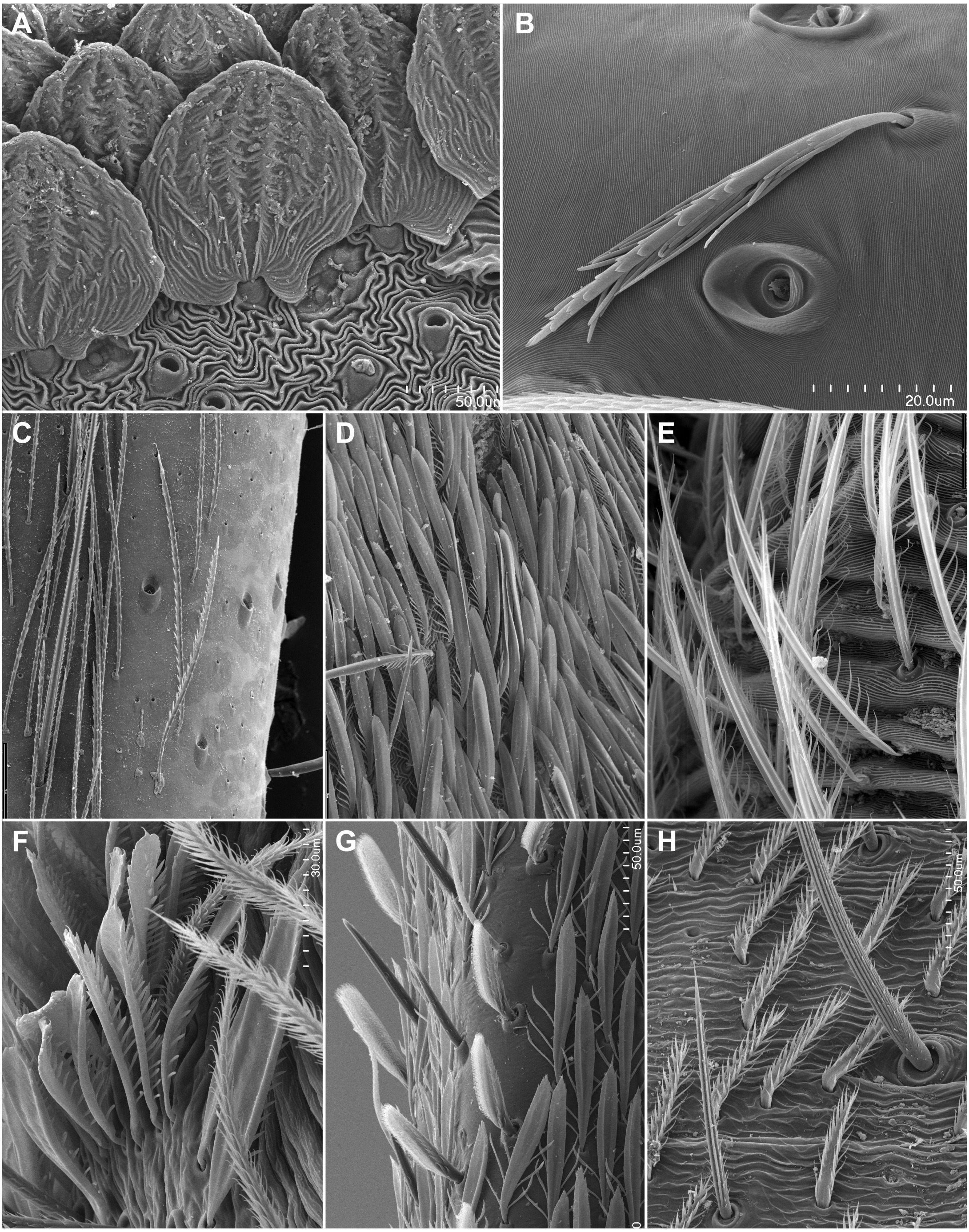


Fig. 93. Scales. **A.** *Hovops* sp. (Selenopidae), female abdomen. **B.** *Apostenus californicus* (Liocranidae), female metatarsus I. **C.** *Anyphaena accentuata* (Anyphaenidae), female tibia I. **D.** *Ammoxenus amphalodes* (Ammoxenidae), male abdomen. **E.** *Rastellus florisbad* (Ammoxenidae), male abdomen. **F.** *Micaria fulgens* (Gnaphosidae), female abdomen. **G.** *Micaria fulgens* (Gnaphosidae), female tibia I. **H.** *Gnaphosa taurica* (Gnaphosidae), female abdomen.

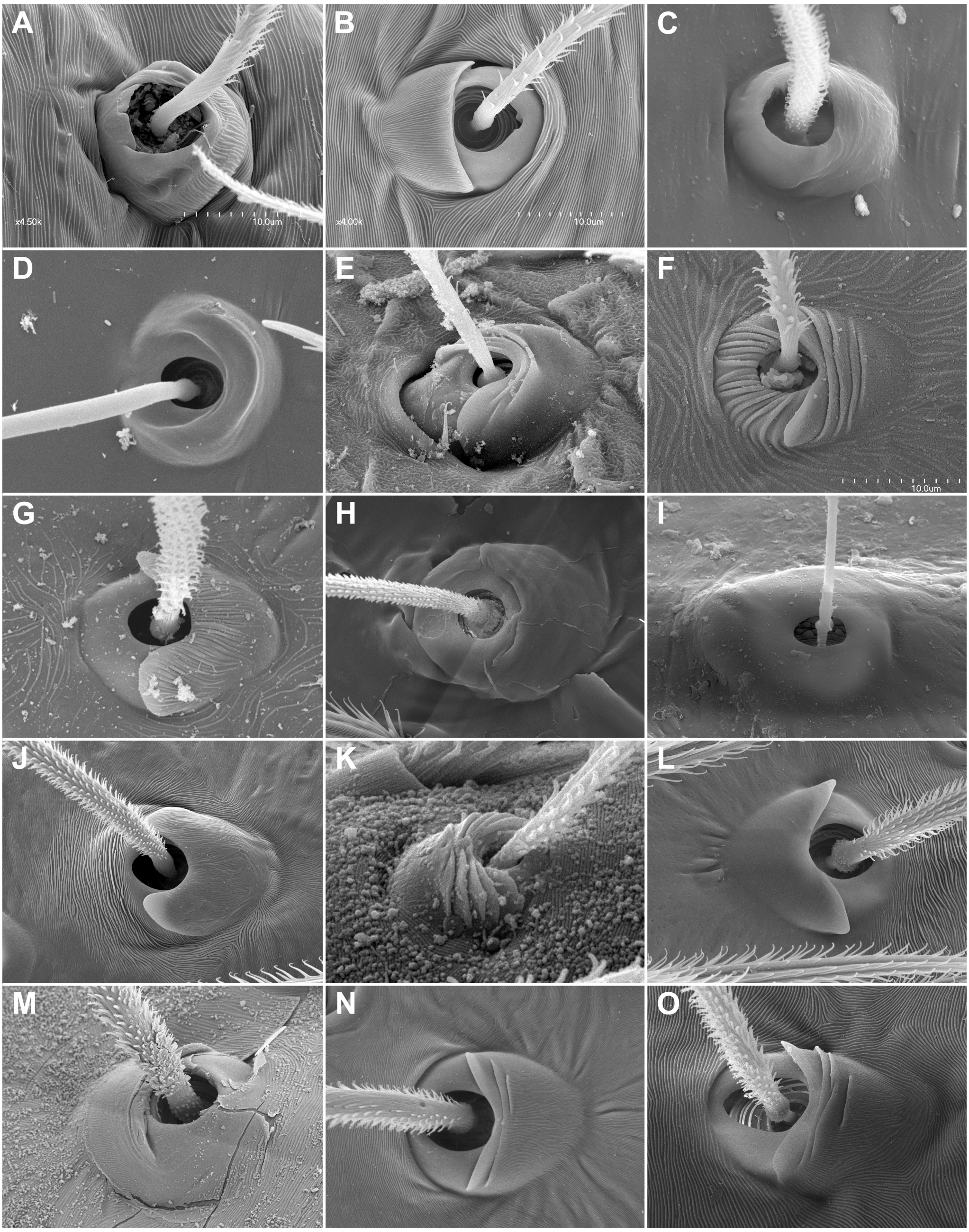


Fig. 94. Trichobotria (except noted, from female legs). **A.** *Hypochilus pococki* (Hypochilidae) leg of early spiderling. **B.** *Austrochilus forsteri* (Austrochilidae) leg of early spiderling. **C.** *Kukulcania hibernalis* (Filistatidae), female palp. **D.** *Ariadna boesenbergi* (Segestriidae). **E.** *Huttonia* sp. (Huttoniidae). **F.** *Pimus napa* (Amaurobiidae). **G.** *Macrobunus multidentatus* (Amaurobiidae). **H.** *Homalonychus theologus* (Homalonychidae). **I.** *Cryptothele alluaudi* (Zodariidae) leg of immature. **J.** *Cycloctenus nelsonensis* (Cycloctenidae). **K.** *Ciniflella* BRA (Tengellidae). **L.** *Trochosa ruricola* (Lycosidae). **M.** *Selenops debilis* (Selenopidae). **N.** *Acanthoctenus* cf. *spinipes* (Ctenidae). **O.** *Zora spinimana* (Miturgidae).

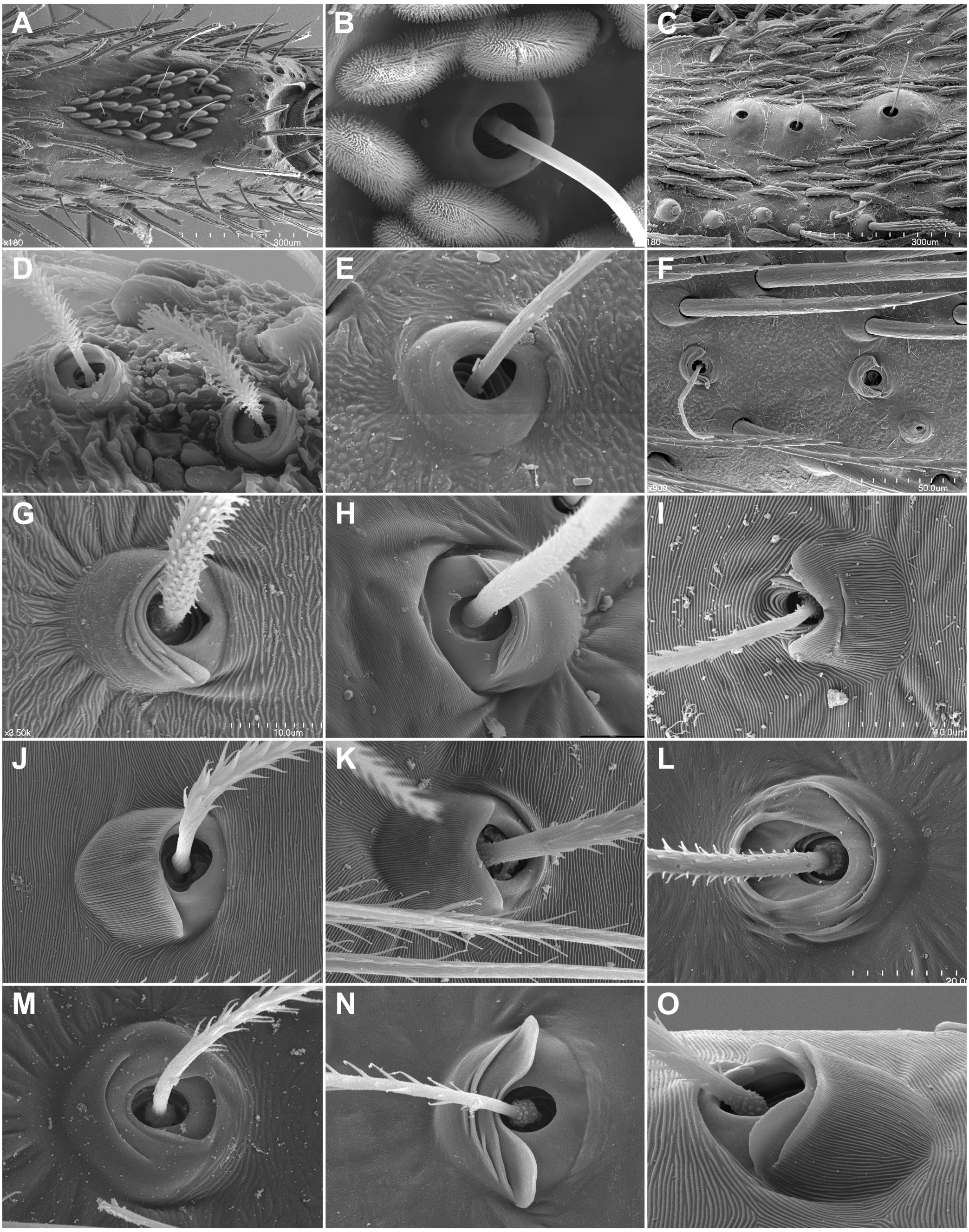


Fig. 95. Trichobotria (except noted, from female legs). **A.** *Borboropactus bituberculatus*. (Thomisidae), depressed field on tip of tarsus I. **B.** Same, detail of trichobothria. **C.** Same, metatarsus I. **D.** *Boliscus* cf. *tuberculatus* (Thomisidae), male palpal tibia. **E.** *Tmarus holmbergi* (Thomisidae). **F.** *Aphantochilus rogersi* (Thomisidae). **G.** *Cocalodes longicornis* (Salticidae). **H.** *Heteropoda venatoria* (Sparassidae), male palpal tibia. **I.** *Hortipes merwei* ("Corinnidae"). **J.** *Malenella nana* (Anyphaenidae). **K.** *Gayenna americana* (Anyphaenidae). **L.** *Corinna bulbula* (Corinnidae). **M.** *Pseudocorinna felix* (Corinnidae). **N.** *Oedignatha* cf. *jocquei* (Liocranidae). **O.** *Apostenus californicus* (Liocranidae).

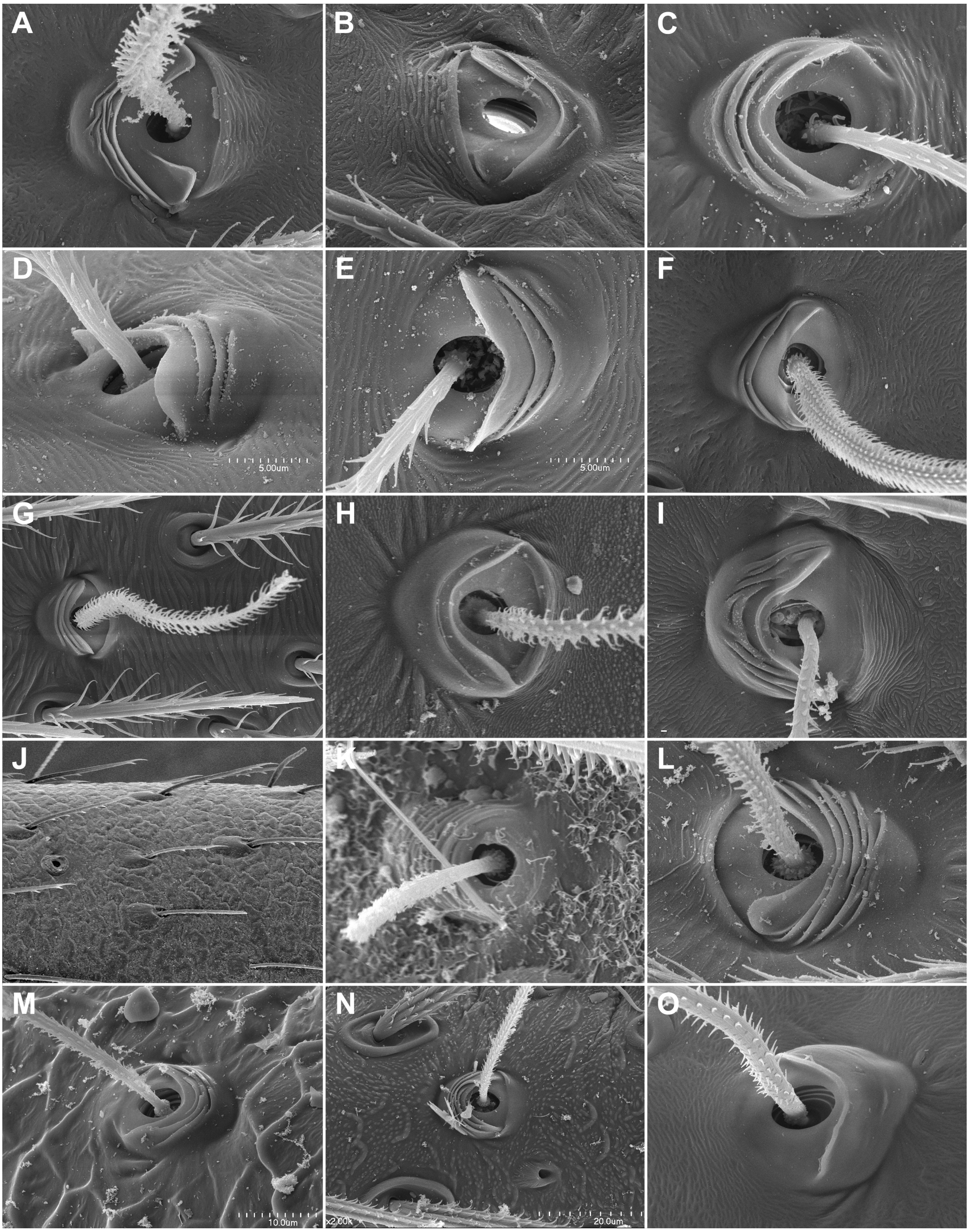


Fig. 96. Trichobotria of female (except noted, from legs). **A.** *Sesieutes* sp. (Liocranidae). **B.** *Jacaena* sp. (Liocranidae). **C.** *Trachelas mexicanus* (Trachelidae). **D.** *Meriola barrosi* (Trachelidae), palpal tibia. **E.** Same. **F.** *Paccius* cf. *scharffi* (Trachelidae). **G.** *Phrurolithus festivus* (Phrurolithidae). **H.** *Desognaphosa yabbra* (Trochanteriidae). **I.** *Legendrena perinet* (Gallieniellidae). **J.** *Galianoella leucostigma* (Gallieniellidae). **K.** *Ammoxenus amphalodes* (Ammoxenidae). **L.** *Centrothele mutica* (Lamponidae). **M.** *Cithaeron delimbatus* (Cithaeronidae), metatarsus I. **N.** Same, tibia I. **O.** *Gnaphosa taurica* (Gnaphosidae).

1970a, 1970b). The distal pore may be protected from direct contact with the substratum by an apical barb (fig. 84E). The chemosensory setae are inserted in a rather regular angle (about 70°) and have an "S" profile (Foelix, 2011). The articulation between shaft and socket is seemingly less movable; in some groups the articulation is totally exposed instead of folded, suggesting that they are not capable of much movement (fig. 85B). In several groups of small spiders and in spiderlings the chemosensory setae around the spinneret spinning fields are very similar to spigots, differing only by their lack of a base (fig. 85A) (see also Lopardo and Hormiga, 2007).

142. Tactile hair type: 0. Plumose or pseudoserrate, with many thin barbs (fig. 85A). 1. Serrate, with few, solid, triangular barbs (figs. 35D, 60A, 95F). See Lehtinen (1975) and (Griswold et al., 2005: char. 17). This is a traditional araneoid character (Lehtinen, 1967: fig. 1; 1975: 27), here also reported for some thomisids. Lehtinen (1975: fig. 7) reported "pseudoserrate" setae in the zodariid *Hermippus*, with similar morphology as in araneoids. COMMENTS: *Nicodamus*: limiting case, close to serrate (scored 0). *Psechrus*: a good example for the "pseudoserrate" problem (scored 0). *Geraesta*, *Xysticus*, *Stephanopis ditissima*, *Tmarus*, *Titidius*: some dorsal tarsal hairs look like serrate (scored 01). *Thomisus*: most leg hairs are thick and smooth, except those at the sides of the claws and one median on top of the claws (scored 0). *Strophius*, *Aphantochilus*: mostly serrate (scored 1).

143. Spination legs I–II dramatically reduced: 0. With spines. 1. Virtually no spines (fig. 48G). COMMENTS: *Hypochilus*: only metatarsi with spines (scored 1). *Oecobius*: Only some sparse spines (from Charles Griswold, in litt.) (scored 01). *Huttonia*: few macrosetae (scored 1). *Cryptothele*: somewhat reduced (scored 01). *Micaria*: absent on tibiae and metatarsi I and II (scored 01). Cf. Eutichuridae QLD: female spines: metatarsus I v p1-p1-p1, metatarsus II v p1 ap; male with more spines, including metatarsus I v 2-2-1 (scored 1). *Cheiracanthium*: tibial spines reduced (scored 0). *Cheiramiona*: spines fairly reduced (scored 01). *Toxoniella*: no spines on tibia (scored 0). *Holcolaetis*: present on femora (scored 01). *Hispo*: only femora p 1ap or p 2ap (scored 1).

144. Spination legs III–IV dramatically reduced: 0. With spines (fig. 48E, F). 1. Virtually no spines (fig. 48H). COMMENTS: *Cyrioctea*: scoring taken from female *C. spinifera*, which has more spinose legs than other congeners. *Prodidomus*: only metatarsi III v 1 ap, IV v 1ap, p 1ap (scored 1). *Ariadna*: IV reduced, not III (scored 01). *Oecobius*: only some sparse spines (from Charles Griswold, in litt.) (scored 01). *Neato*: a few spines only on leg III (scored 1). *Cheiramiona*: Reduction intermediate (scored 01). *Vectius*: bristles in male are more like macrosetae, in thickness and in position (scored 1). *Platyoides*: only bristles, but not in the usual stereotyped position of macrosetae (scored 1).

145. Prolateral series of macrosetae on leg I: 0. Absent, prolateral macrosetae not organized in one row. 1. Several series of macrosetae with increasing length, as in mimetids. This character was mainly used to record the absence of a mimetid synapomorphy throughout the ingroup taxa. *Araneus diadematus* has some prolateral macrosetae roughly in a line, but not so well organized as in mimetids (scored 0).

146. Femoral dorsal median line of macrosetae: 0. Present, at least one macroseta (fig. 48E, F). 1. No dorsal median macroseta (fig. 48H). COMMENTS: *Ariadna*: many dorsal spines in male, none on female (scored 01). *Oecobius*: d 1ap (scored 0). *Megadictyna*: d 1-0 (scored 0). *Brachyphaea*: male right IV d 1bas (scored 01). *Pseudocorinna*: I d 1, III or III and IV d 1ap (scored 0). *Phrurotimpus*: one basal on all legs (scored 0). *Teutamus*: only prolaterals, on I and II (scored 1). *Jacaena*: IV d 1bas (scored 0). *Sesieutes*: IV d 1bas (scored 0). *Oedignatha*: II d 1bas (scored 0). *Vectius*: only bristles, the basal dorsals on femora may be closer to macrosetae (scored 1). *Centrothele*, *Legendrena*: I–IV d 1bas (scored 0). *Austrachelas*: present on leg IV, those of leg I reduced to bristles (scored 0). *Cithaeron*: basal dorsal present on all legs (scored 0). *Cheiracanthium*: only p and r (scored 1).

MACROSETAE PATTERNS

Ramírez (2003: 51) described a conserved pattern of distribution of macrosetae (= spines) for Anyphaenidae:

> In most genera the spines on leg I are similarly distributed to those on leg II. Legs III and IV are also similar in spines, which are more numerous than on forelegs. Through the four pairs of legs, most spine positions are conserved, because they are serially homologous. A common pattern is:
>
> Legs I and II, femur d 1-1-1, p 0-1-(1-d1), r d1ap; tibia v 2-2-2; metatarsus v 2bas. III, femur d 1-1-1, p and r 0-d1-d1; patella r d1; tibia v 2-2-2, p and r d1-1, d r1bas; metatarsus v 2-2-2, p and r d1-1-1, d 0-p1-2. IV, femur d 1-1-1, p 0-d1-d1, r d1ap; patella, tibia, and metatarsus = III.
>
> In some groups the anterior legs are almost as spinose as the posterior legs. A common pattern of this type is:
>
> Leg I and II, femur d 1-1-1, p and r 0-d1-(1-d1); tibia v 2-2-2, p and r d1-1, d r1-0-1-0; metatarsus v 2bas, p and r d1-1-1, d 0-p1-2. III, femur = I; patella r d1; tibia = I; metatarsus = I, but v 2-2-2. IV, femur d 1-1-1, p 0-d1-d1, r d1ap; patella, tibia, and metatarsus = III.
>
> Most spine patterns vary between these two examples. In the spinose pattern, spines on anterior and posterior legs differ mostly by the ventrals on metatarsi. There are only a few species with more than a single pair of ventral spines on metatarsus I or II, they are not especially spinose on other surfaces, and these spines are not usually sexually dimorphic. Some species have more than three pairs of ventral spines on tibiae I and II, conferring a raptorial appearance (e.g., some *Monapia*).
>
> Males are often more spinose than are females. The additional male spines appear after the last ecdysis. Spines of penultimates of both sexes are similar to those of the female. In some rare specimens (but commonly in *Sanogasta backhauseni*) there are supernumerary spines, for example, two or three spines where one is expected. Such an anomaly is often asymmetrical.
>
> Bristles (similar to spines but thinner and shorter) seem to be homologous to spines, because some specimens have a bristle where a spine is normally found. Frequent positions for replacement of spines by bristles are the prolaterals and retrolaterals on femora, and the v p1-x-x of tibia II. In species with spinose males, it is common that the male has a spine where the female has a bristle; common positions are the dorsals of tibiae (r1-0-1-0) and patellae (1-0-1).

This stereotyped pattern turned out to be applicable to many other spider families, and seems to be a synapomorphy of the entire RTA clade. In this pattern the macrosetae on femora, tibiae, and metatarsi are placed in clearly defined thirds, and hence is here named the *x-x-x pattern*. This regularity pervaded some nomenclature used to describe macrosetae patterns. For example, the nomenclature introduced by Platnick and Shadab (1975) reports counts of macrosetae grouped in thirds of leg articles. The outgroups of the RTA clade do not follow this pattern of thirds, and are often more spinose.

147. General femoral spination pattern: 0. More than x-x-x (fig. 48B). Outgroups of the RTA clade typically have a nonstereotyped spination, with, e.g., more than three median dorsal spines. This is also true in some large spiders with long legs, where the pattern of the RTA clade is seemingly stretched to four or more positions. 1. x-x-x (fig. 48D, C). The femoral spines are distributed in a stereotyped pattern, with a repeated distribution in thirds, more evident in, but not exclusive of, the dorsal median line of spines. COMMENTS: *Filistata*: reduced, I–VI d 1bas, I also p d1 (scored -). *Ariadna*: no dorsals (scored -). *Oecobius*: *Uroctea* similar to *Araneus* (scored -). *Uloborus*: reduced (scored -). *Araneus*: much more, d 1-1-1-1-1 (scored 0). *Mimetus*: much more, d 1-1-1-1-1. I and II with posterior and anterior lines of short macrosetae (scored 0). *Megadictyna*: reduced (scored 01). *Nicodamus*: medians in zig-zag plus many prolaterals (scored 0). *Titanoeca*, *Pronophaea*, *Procopius*, *Mandaneta*, *Phrurolithus*, *Jacaena*, *Sesieutes*, *Oedignatha*: reduced spination (scored -). *Desis*, *Storenomorpha*, *Orthobula*: no spines (scored -). *Homalonychus*: approximately d 1-1-0, p and r d1-1-d1-01 (scored 1). *Psechrus*: more spines because very long femora (scored 0). *Zoropsis*: p and r 0-1-1-1-1 (scored 0). *Senoculus*: several p and r, but d 1-1-1 (scored 1). *Pseudocorinna*: d 1ap (scored -). *Phrurotimpus*: femora d 1-0-0 (scored -). *Otacilia*: 1-1 or 1-0 (scored -). *Neozimiris*: d 1-1-0 (scored 1). Cf. *Moreno* ARG: d 1-1-0. Some reductions also in tibiae and metatarsi (scored 1). *Desognaphosa*: 1-0-1 (scored -). Cf. Eutichuridae QLD: still reduced in male (scored -). *Lessertina*: several dorsals, very short, on a median line (scored -). *Miturga gilva, Syspira*: p and r 0-1-1-1-1 (scored 1). *Eusparassus*: d 1-1-1, p and r with some intermediates as well (scored 1). *Cebrenninus*: 0-1-1 (scored 1). *Geraesta*, *Stephanopis ditissima*: d 0-1-1 (scored 1). *Borboropactus*: III–IV no spines (scored -). *Aphantochilus*: small spines with strange pattern (scored -). *Galianoella*: d 1-1-0 (scored -). *Holcolaetis*, *Portia*: 0-x-x-x (scored 1).

148. General tibial spination pattern: 0. More than x-x-x (fig. 48A). 1. x-x-x (fig. 48E). COMMENTS: *Filistata*: a line of 3–4 prolateral ventral spines (scored -). *Thaida*: e.g., 2-2-2-2 instead of 2-2-2 (scored 0). *Ariadna*: from tibia III (scored 1). *Oecobius*: *Uroctea* similar to *Araneus* (scored -). *Eresus*: female reduced (scored 0). *Uloborus*: irregular (scored 01). *Araneus*: four ventral pairs (scored 0). *Megadictyna*: spines more or less anphaenidlike, but four pairs (scored 0). *Titanoeca*, *Dictyna*, *Cryptothele*, *Pronophaea*, Eutichuridae MAD, *Phrurotimpus*: reduced (scored -). *Storenomorpha*: none (scored -). *Homalonychus*: some additional v, no d (scored 0). *Psechrus*: more spines because very long tibia (scored 0). *Pseudoctenus*: anterior legs with many spines (scored 1). *Copa*: all leg macrosetae very long (scored 1). *Brachyphaea*: reduced, only the ventrals present, compatible with state 1 (scored -). *Pseudocorinna*: posteriors reduced (scored -). *Neozimiris*: only v and p (scored 1). *Ammoxenus*: additional spines but still on the same pattern (scored 1). Cf. Eutichuridae QLD: still reduced in male (scored -). *Cheiramiona*: reduced (scored -). *Cebrenninus*: 0-2-2-2 (scored 1). *Borboropactus*: III–IV no spines (scored -). *Tmarus*: short, 0-x-x or so (scored -). *Aphantochilus*: small spines with strange pattern (scored -).

149. General metatarsal spination pattern: 0. Leg III more than x-x-x or irregular. 1. x-x-x. This character is defined on metatarsus III, as the I and II frequently have many fewer spines, and the IV may be modified by the calamistrum. COMMENTS: *Hypochilus*: several spines irregularly disposed (scored 0). *Filistata*: four pairs irregularly paired (scored 0). *Ariadna*: reduced (scored 1). *Oecobius*: *Uroctea* similar to *Araneus* (scored -). *Araneus*: four ventral pairs on III, prolateral line on IV (scored 0). *Megadictyna*: spines more or less anphaenidlike, but four pairs, much more and different on male (scored 0). *Nicodamus*: two ventral lines close together plus a prolateral ventral line (scored 0). *Titanoeca*: v 2-2-2-1 (scored 0). *Dictyna*: very few spines (scored -). *Cryptothele*, *Lessertina*, *Pronophaea*, *Phrurotimpus*, *Neozimiris*, *Stephanopis ditissima*: Reduced (scored -). *Storenomorpha*: only v 2 ap (scored -). *Brachyphaea*: reduced, only the ventrals present, compatible with state 1 (scored -). *Pseudocorinna*: posterior legs reduced spination (scored -). *Ammoxenus*: additional spines but still on the same pattern (scored 1). *Selenops*: no dorsals and few laterals (scored 1). *Hovops*: reduced v 2-0-0 (scored -). *Cebrenninus*: 0-2-2 (scored 1). *Borboropactus*: III–IV no spines (scored -). *Tmarus*: short, 0-x-x or so (scored -). *Aphantochilus*: small spines with strange pattern (scored -). Cf. Eutichuridae QLD: from male (scored 1).

150. Female leg cuspules (= short macrosetae): 0. Absent. 1. Present. Cuspules are very short macrosetae (fig. 86F) typical of many Trachelidae, most often in males. A few female trachelids (and also the zodariid *Storenomorpha*!) also have cuspules. COMMENTS: *Paccius*: I and II, metatarsus and tarsus (scored 1).

151. Sexually dimorphic leg macrosetae-cuspules: 0. Leg cuspules absent. 1. Macrosetae with bulbous base and thin shaft in male (fig. 86C, D). *Brachyphaea* has sexually dimorphic macrosetae, reduced in the male (compare with fig. 86A, B). 2. Macrosetae reduced to cuspules in male (fig. 86E). States are unordered, although the male macrosetae reduction in *Brachyphaea* is a good candidate of intermediacy toward the more extreme sex dimorphism found in Trachelidae. COMMENTS: *Cybaeodamus*, *Gayenna*: males with anterior legs much more spinose (scored 0). *Trachelas mexicanus*: cuspules also present in female, but more abundant in male (scored 2). *Paccius*: cuspules also present in females (scored 2). *Paravulsor*: macrosetae and cuspules in male metatarsus I (one row v prolat), tarsus I (group at base), metatarsus II (one row of thick hairs v prolat) (scored 1). *Thomisus*: male without macrosetae (scored ?).

152. Tarsal macrosetae: 0. Absent. 1. Present. Among Araneomorphae, tarsal macrosetae are more common in lower entelegynae and orbicularians. See following characters for specific configurations of tarsal macrosetae (chars. 153, 154). COMMENTS: *Megadictyna*: at least one (Griswold et al., 2005: fig. 137B) (scored 1). *Desis*: on

III and IV (scored 1). *Cyrioctea*: on posterior legs (scored 1). *Cryptothele*: just thick setae (scored 0). *Meriola*, *Trachelas mexicanus*, *Paccius*: cusps (scored 1). *Trachelopachys*: cusps tarsi I, II (scored 1). *Orthobula,* cf. *Moreno* ARG: tenent macrosetae (scored 1).

153. Tarsus IV comb: 0. Absent. 1. Present, line of blunt macrosetae. Only *Uloborus* in this dataset (see Griswold et al., 2005: 50). COMMENTS: *Oecobius*: several macrosetae, not in a line (scored 0). *Megadictyna*: ventral side uniformly covered by macrosetae, more dispersed in male (scored 0). *Nicodamus*: some thick setae, not in a comb (scored 0). *Badumna*: one ventral median short macroseta (scored 0). *Homalonychus*: the rows of thick setae (not macrosetae) are not combs (scored 0). *Eilica*: two ventral lines of slightly thicker setae (scored 01). Cf. *Moreno* ARG: the tenent spines are on anterior legs (scored 0). *Thomisus*: tarsus I with two ventral lines of thick setae (scored 0).

154. Sustentaculum: 0. Absent. 1. Present. Here defined after comparison with *Araneus*, as an apical, ventral prolateral macroseta (fig. 60A, B) proximal to the membranous division at base of claws. Note that the sustentaculum as defined by Schütt (2002: fig. 16) is retrolateral and serrate, different to that from Scharff and Coddington (1997), ventral-prolateral. COMMENTS: *Filistata*: several macrosetae, a pair apical ventral (scored 01). *Stegodyphus*: several macrosetae in that area (scored 01). *Oecobius*: one short prolateral macroseta, just proximal to the unsclerotized suture of the claw area, and several retrolateral ones (scored 01). *Uloborus*: at least one ventral prolateral macroseta (fig. 59F) (scored 01). *Mimetus*: there are both ventral-prolateral and retrolateral macrosetae (scored 01). *Dictyna*: one retrolateral and one median ventral apical macrosetae (scored 01). *Neoramia*: there is a retrolateral apical macroseta (scored 0). *Desis*: several ventral distal spines on tarsus III and IV (scored 01). *Toxopsiella*: ventral apical setae with extremely long tips (fig. 62A) (scored 0).

155. Macrosetae with apical tenent surface on leg I: 0. Absent. 1. Present. In *Orthobula* the leg macrosetae have a ventral tenent surface on the tip, exactly as the one found in scopular setae (fig. 86G, H). In cf. *Moreno* ARG the scopular setae are very strong, and cooccur with regular macrosetae in the metatarsus and tibia (fig. 88A–C, E, F). In *Apostenus* the thick scopular setae occur on the tarsus, and the metatarsus and tibia have normal macrosetae only (fig. 87A–C). These setae of intermediate morphology between scopular seta and macroseta were described by Ubick and Platnick (1991, as "bristles"), and proposed as a potential synapomorphy of Liocraninae plus Phrurolithinae. There seems to be a continuous variation, from the relatively thin setae of *Apostenus* (fig. 87C), to the large macrosetae of *Orthobula* (fig. 86G). The homology hypothesis used here is different from the one proposed by Ubick and Platnick (1991). Here the tenent tip in the macrosetae of *Orthobula* is scored as state 1, but the thinner setae of *Drassinella* (fig. 87D, E) are scored as intermediate (01). The tenent setae in *Liocranum* (fig. 87F, G) are here considered regular scopular setae, along with other examples of thin scopular setae (figs. 89G, 91C–F). COMMENTS: *Tengella*, *Uliodon*, *Paccius*, *Neoanagraphis*, *Fissarena*: thin scopular setae (scored 0). *Homalonychus*: compressed setae, similar as in claw tuft (scored 0). *Centrothele*: those of tibia slightly thinner (scored 0). *Trachelas minor*: the scopular hairs have some resemblance to macrosetae (scored 0). Cf. *Moreno* ARG: present, in addition to the scopular setae. *Orthobula*: only tenent spines, no scopula (scored 1). *Drassinella*: intermediate, rather thin, not aligned (fig. 87E) (scored 01).

156. Row of spines between AER and PER: 0. Absent. 1. Present, a synapomorphy of *Cyrioctea* (fig. 12E); there is also a weaker line on the clypeus.

157. Scales: 0. Absent. 1. Present. Scales can be feathery (fig. 92D, F), almost cylindrical (figs. 92B, 93C) or intermediate between those shapes (figs. 91F, 92H, 93B, D), or flat (figs. 92C, 93A), among other shapes. COMMENTS: *Thaida*: Comparatively very large and thick. Perhaps identified only as scales because of the setules (fig. 92A) (scored 1). *Eriauchenius*: those of dorsum of abdomen interpreted as setae (scored 0). *Metaltella*, *Badumna*: from stereomicroscope only (scored 1). *Storenomorpha*: Forming white band on carapace. Seen on compound microscope. However, the white setae on legs, e.g., the apical crown dorsal on metatarsi, are similar to normal setae under SEM examination, and are tentatively interpreted as normal hairs (scored 1). *Oxyopes*: scored from chelicerae and epigynum (scored 1). *Cycloctenus*: looking like scales with the stereomicroscope, they lack the basal angle (scored 0). *Toxopsiella*: white scales with compound microscope, not scanned (scored 1). *Corinna*: no leg scales with SEM (scored 0). Cf. *Medmassa* THA: scales are tentatively identified as the feathery setae shorter than hairs, but they are thick and lack the bending at the base (fig. 92E) (scored 1). *Phrurotimpus*: one observed with SEM on distal patella (scored 1). *Otacilia*: large sockets seen (fig. 55F) (scored 1). *Hortipes, Gnaphosa, Neozimiris*: scored from abdominal scales (scored 1). Cf. *Moreno* ARG: Perhaps more than one type. Abdomen with *Gnaphosa*-like setae (two longitudinal axes), carapace with something different. Here scored those of carapace (scored 1). Cf. Gnaphosoidea TEX: the most common abdominal setae have two ribs as in gnaposid scales, but are considered hairs here (scored 0). *Centrothele*: from legs, scales of a very strange kind (fig. 91F) (scored 1). *Neato*: from stereomicroscope (scored 0). *Raecius*: from Griswold (2002) (scored 1). *Cebrenninus*, *Epidius*: not found with SEM (scored 0). *Stephanopis ditissima*: whitish scales, ventral side with spines apparently to stuck dirt (scored 1).

158. Scale axis flattened: 0. Axis cylindrical (fig. 92B, F). 1. Axis or entire scale flattened (figs. 91F, 92C, H, 93A, D). COMMENTS: *Senoculus*: see also Griswold (1993: fig. 61) (scored 1). *Griswoldia*: perhaps two kinds of scales, but only the ones with smaller sockets here interpreted as scales (Griswold, 1991: fig. 32, bottom left) (scored 0). *Ciniflella* BRA, *Ciniflella* ARG: only slightly flattened (scored 01). *Holcolaetis*, *Portia*, *Plexippus*: intermediate (fig. 92I) (scored 01).

159. Scale setules: 0. Absent. The scales have only short barbs (fig. 92B). 1. Present (fig. 92D). Setules are long barbs as in feathery setae. COMMENTS: *Apostenus*: parallel to axis! (fig. 93B) (scored 1). *Syspira*: some short basal setules (fig. 92G) (scored 01). *Ciniflella* ARG: Basal short setules (scored 01). *Odo bruchi*: two types of scales occurring together on abdomen (fig. 102D) (scored 01). *Plexippus*: just long spines, might be intermediate—three kind of scales! (scored 0).

160. Scales axes, number: 0. One. This applies also to cylindrical scales (fig. 92B, F). 1. Two (fig. 93G, H). 2. Three (figs. 92C, 93E). States were considered unordered. COMMENTS: *Tengella*: dorsal spines gradually aligning in two lines through apex (scored 0). *Micaria*: leg scales with two ribs, abdominal scales with an incipient median rib (fig. 93F) (scored 01).

161. Tarsal scopula of tenent setae: 0. Absent. 1. Present, setae with a pad of tenent barbs (see distinction between scopula and claw tuft under char. 163). True tenent setae have a surface with barbs widened at the tip (fig. 89I). The scopular hairs have a distal surface with tenent barbs, and are usually rounded or truncate at the tip (figs. 86F, 90E, 90F, 91A), but the tip may be acute instead (fig. 89E). In large spiders the setae are often more elongate (fig. 89D, H). With the scopular setae there seems to be an intermediate morphology of pseudotenent setae with a filiform end (fig. 61H), as occurs with the claw tuft (see char. 163). Because the pattern is similar as in the claw tuft, and there are several less clear intermediates between tenent and pseudotenent, state (1) covers all scopular setae with tenent barbs, regardless of the setal tip being acute, rounded or more truncate. COMMENTS: *Cybaeodamus*: pseudotenent-looking setae, but tip of barbs acute, long, and curved (fig. 89B, C) instead of expanded, probably some adhesive effect similar as in *Sicarius* and *Homalonychus* (Duncan et al., 2007) (scored 0). *Storenomorpha*: very plumose hairs (scored 0). *Pseudolampona*: a few tenent setae on distal half (scored 1). *Zoropsis*: perhaps pseudotenent, tenent barbs not seen (scored 01). *Uliodon*, *Liocranoides*: pseudotenent, tenent barbs, and acute seta tip (scored 1). *Lauricius*: elliptical tenent pads, rounded tips (fig. 89D) (scored 1). *Zorocrates:* rounded tips with a thin apical filament, intermediate between normal spatulate and pseudotenent (scored 1). *Hovops*: just a few (scored 1). *Cebrenninus, Epidius*: apparently pseudotenent (scored 1). *Borboropactus*, *Geraesta*, *Stephanopis ditissima*, *Stephanopoides*, *Boliscus*, *Xysticus*: pseudotenent-like setae, but tip of barbs acute (fig. 90A–D) (scored 0).

162. Scopula seta socket indented: 0. Absent (fig. 89J). 1. Present (figs. 57D, 87G, 91B). Ubick and Platnick (1991) commented that the pronounced ectal projection is related to bristle erection. It seems that Bosselaers and Jocqué (2000) scored scopular setae as their character 4 ("rows of bristles, implanted in basal, cuplike sockets, ventrally on ta, mt and often ti of legs I and II. The tips of these plumose bristles are spatula-, spoon-, or clubshaped"). COMMENTS: *Huttonia*: more obtuse projection (scored 1). *Storenomorpha*: plumose setae, but not indented (scored -). *Meriola*: not indented on tibia! (scored 1). *Olbus*: *O. eryngiophilus, O. nahuelbuta* from Ramírez et al. (2001) (scored 0). *Fissarena*: although Henschel et al. (1995) mentioned "heart-shaped scopula hairs," I could not see anything particular about them to match that description (fig. 91E) (scored 0).

163. Claw tuft: 0. Absent (fig. 45A). 1. Of pseudotenent setae, with acute tip. Some thomisids and miturgids, among others, have expanded barbs as in tenent setae, but the tip of the seta is still acute (figs. 61G, 64C–E). 2. Of tenent setae with widened tip (figs. 63E, 66E, 67B). A claw tuft is here recognized as one or more tenent setae arising at each side of the claws. Typical claw tufts have a bunch of tenent setae, especially in large or medium sized spiders, but the tenent setae are relatively larger, and the claw tufts less dense, in small species (fig. 81B). The claw tuft may arise from a plate well delimited by contiguous areas of flexible cuticle (figs. 63A, 67C), from a plate slightly delimited by sutures (fig. 67B), or from an area continuous with the hard tarsal cuticle (fig. 80A). In some species there is an incipient claw tuft made of a more compact, apical group of scopular setae (figs. 62C, 63F, 80E). Here a true claw tuft is identified by two conditions: (1) being composed of tenent or pseudotenent setae, and (2) having a clear transition from the ventral-lateral cuticle or setae. Such a transition occurs when the claw tuft arises from a delimited basal plate or by a difference in the tenent setae themselves (e.g., larger setae in the claw tuft, relative to the ventral-lateral scopula). Some terminals in this dataset were scored as ambiguous (*Griswoldia*, *Lauricius*, *Paravulsor*, several Miturgidae, and *Centrothele*). The claw tufts of *Homalonychus* are tentatively scored as true tenent setae because they have tenent barbs and somewhat blunt tips, although their morphology is peculiar (fig. 61B–D), and living specimens are unable to walk on vertical glass surfaces (personal obs.). COMMENTS: *Homalonychus*: MJR562 did not walk on glass (scored 2). *Dolomedes*: absent, but *Dossenus* has something quite like claw tufts, yet another convergence (Estevam Luis Cruz da Silva, in litt., to Diana Silva Dávila, 30 Jan. 2006) (scored 0). *Clubiona*: Leg I looks intermediate with scopula, but very clear tuft under the stereomicroscope (the hairs are different). Leg leg IV with a well-separated claw tuft plate, as in *Elaver* (scored 2). *Elaver*: leg IV claw tuft well developed (scored 2). *Toxoniella*, *Phrurolithus*, *Phrurotimpus*, *Otacilia*, *Drassinella*, *Orthobula*, *Oedignatha*, *Micaria*, *Neozimiris*, *Lygromma*, *Ammoxenus*, *Cithaeron*, *Anyphaena*, *Gayenna*, *Amaurobioides*, *Cocalodes*, cf. *Moreno* ARG: sparse tuft (scored 2). *Teutamus*: tenent setae fused at base, with very thin shaft (scored 1). *Prodidomus*: Sparse tuft. Large setae similar as those of *Homalonychus* (scored 2). *Gnaphosa*: three or four tenent setae on leg I, one on leg IV (fig. 83A) (scored 2). *Pseudolampona*: just a few tenent setae in a well delimited patch (scored 2). *Lampona*: limiting case (scored 2). *Austrachelas*: a small but well delimited patch with larger setae (scored 2). *Centrothele*: sparse, intermediate (scored 02). *Neato*: one bent, not tenent seta, as in *Meedo* (scored 0). *Miturga* cf. *lineata*, *Miturga gilva*, *Teminius*, *Syspira*, *Lauricius*: not well-defined plate, the apical tenent setae have rather acute tips, more acute than those of the scopula, intermediate between spatulate and pseudotenent (scored 012). *Mituliodon*, Miturgidae QLD: the apical tenent setae have rather acute tips, more acute than those of the scopula, intermediate between spatulate and pseudotenent (scored 12). *Griswoldia*: intermediate with scopula (scored 01). *Zorocrates*: scopula of pseudotenent setae (scored 0). *Odo bruchi*: interpreted as a scopula reaching the claws (scored 0). *Paravulsor*: intermediate, mostly with acute tip, but there are setae with wide tip plus short acute extension (scored 12). *Epidius*: Benjamin (2000) reported that they walk on glass (scored 1). *Borboropactus*: densely barbed setae with acute tip, but the barbs lack expanded tips (fig. 64B) (scored 0).

164. Claw tuft seta basal section folds: 0. Basal section nearly cylindrical (figs. 61F, 65E, 69F, 80C) or flattened without folds (fig. 80B, C). 1. Basal section with folds or ribs (figs. 71D, E, 72B, 76B, 81B, 83C). COMMENTS: *Trachelas mexicanus*: this seems to be the only case of being not folded at base in Trachelidae (fig. 73E) (scored 0). *Anyphaena*: base cylindrical, thick, folded thereafter (scored 0). *Miturga* cf. *lineata, Miturga gilva*, *Teminius*, *Syspira*: claw tuft details scored, although the interpretation is ambiguous (might be interpreted as an advanced scopula) (scored 0). *Philodromus*: similar to anyphaenids (scored 0).

165. Claw tuft seta base thickness: 0. Thin, the setal shaft is not expanded immediately above the socket (figs. 63B, 69D). 1. Thickened near the socket (figs. 71D, 73E, 77B, E, 80B, C). COMMENTS: *Griswoldia*: from *G. punctata* (Griswold, 1991: fig. 22) (scored 0). *Gayenna*, *Xiruana*: not very thick basally (scored 0). *Anyphaena*: short transition from thin socket to widened portion (scored 01). *Miturga* cf. *lineata*: claw tuft details scored, although the interpretation is ambiguous (might be interpreted as an advanced scopula) (scored 0).

166. Claw tuft setae bases packing: 0. Bases inserted in individual sockets (figs. 63B, C, 69F). 1. Bases packed together (figs. 71B, F, 72B, 76A, B, 79A, B, 76D, 76E, 81C). 2. Bases fused (figs. 74C, D, 70C–E). COMMENTS: *Donuea*: bases appressed but on individual sockets (scored 0). *Apostenus*: only one seta on each side, inapplicable (scored -). *Phrurolithus*: perhaps not even sockets! (scored 1). *Orthobula*: not fused but tightly appressed (fig. 76D) (scored 0). *Micaria*: only two setae, intermediate (scored 01). *Lygromma*, *Cithaeron*, *Austrachelas*: packed but detachable (scored 1). *Ammoxenus*: very slightly packed, only three setae, the superior one somewhat separate on a larger socket (scored 01). *Rastellus*: very slightly packed (scored 01). *Cithaeron*: as in *Lygromma*, detachable (scored 1).

167. Claw tuft base rectangular blocks: 0. Cylindrical, folded, or irregularly widened. 1. Rectangular blocks, as in Trachelidae (figs. 72B, E, 73C, E, 74B). The most basal portion of the seta, at its insertion, is widely expanded in large blocks with defined vertices (see arrows of fig. 73C). COMMENTS: *Trachelas minor*: intermediate, most ventral seta more blocklike, the rest more folded (fig. 72G) (scored 01). *Eilica*: wide flattened base (scored 0).

168. Claw tuft seta tip profile: 0. Not indented (figs. 61E, 65A, 69B, C, G, 75C, 77C, 80D). 1. Deeply indented (fig. 68D, I). This synapomorphy of Sparassidae was noted by Simon (1892: 26, fig. 40), although he reported them as scopular, instead of claw tuft setae. This character was brought to my attention by Facundo Labarque (MACN). COMMENTS: *Teutamus*: thin apex (scored ?).

169. Claw–claw tuft clasping mechanism: 0. Absent (fig. 74A). 1. Present (figs. 71A, B, F, 76B, 77D, 78C, D, 81D, C, 83D). The claw base has a ventral prolongation that clasps a folding of a widened claw tuft seta base. This character, in the specific shape of several teeth appressed together (see char. 170 below), was first noted in Platnick et al. (2005: figs. 5–10) and proposed as a synapomorphy of tricongiine Theuminae (Prodidomidae). COMMENTS: *Orthobula*: scored from leg IV (scored 1). *Prodidomus*: same basal extension as in *Neozimiris* (scored 1). *Pseudolampona*: the claw base is flat, projecting, suggestive of a relict of a clasping mechanism (scored 0).

170. Claw–claw tuft clasping mechanism structure: 0. Teeth appressed together (figs. 72F, 73F, 81C, E–G, 83B); Platnick et al., 2005: figs. 5–10). 1. Solid (figs. 71A, B, F, 76B, 78D, 82A, 83D). COMMENTS: cf. Liocranidae LIB: clasp is very thin (scored 1). Cf. *Moreno* ARG: first illustrated in Platnick et al. (2005: figs. 9–10) (scored 0).

171. Claw lever file–claw tuft bases interlocking: 0. Not interlocking (figs. 69A, D, 75A, 80F). 1. Interlocking (figs. 72C, D, 73D, G, 74A, B). The ridges on the claw lever file engage with the bases of the most ventral claw tuft setae, which have mesal extensions matching the ridges. COMMENTS: *Trachelas mexicanus*: the basal border matches the ridges (fig. 73D) (scored 1). *Trachelas minor*: only the first seta interlocking, the claw lever is more ventral, but the morphology is similar to that in other trachelids (scored 1). *Oedignatha*: claw lever smooth (scored 0). *Prodidomus*: claw lever apparently without striations (scored 0). *Neozimiris*: apparently only two shallow striations, but the image is deficient for this (scored 0). *Griswoldia*: from *G. punctata* (Griswold, 1991: fig. 22) (scored 0).

172. Claw tuft setae tenent surface orientation: 0. Facing ventrally (figs. 66E, 67A). 1. Facing mesally (figs. 65F, D, 77A, 81A, 82C). COMMENTS: *Prodidomus*: a dorsal rib on top of the tenent surface (fig. 82C, E) (scored 0). *Micaria*: two large, obliquely oriented, two small, ventrally oriented (fig. 83C) (scored 01).

173. Claw tuft insertion: 0. Continuous with lateral cuticle (figs. 63G, 71A, 72A, 73H). 1. Delimited plate, separated by soft area or furrow from lateral cuticle (figs. 63A, 66A, 67C). The movable plates have been called "tenent plates" by Hill (2006; see also Raven and Stumkat, 2005: char. 46). In *Oedignatha* the claw tuft plate is a finger-shaped projection, with sparse setae on its distal side (fig. 70A, B). COMMENTS: *Clubiona*: partial division (scored 01). *Phrurolithus*, *Phrurotimpus*, *Otacilia*, *Drassinella*, Trachelidae ARG: sockets not defined, single insertion area partially articulate (scored 01). *Teutamus*: single socket (scored 0). *Oedignatha*: a finger-shaped projection with setae on distal side (scored 1). *Centrothele*, *Ammoxenus*, *Cithaeron*: intermediate, thin suture (figs. 77B, 80E) (scored 01). *Clubiona*: partial division (fig. 67B) (scored 01).

174. Membranous extensions of tarsi enclosing claw tuft plate: 0. Absent (figs. 61F, 63A, D). 1. Present (fig. 68A, C, F, G). This character was considered inapplicable for those terminals without a delimited claw tuft plate (see char. 173); it is a further synapomorphy for Sparassidae. COMMENTS: *Brachyphaea*: extended, pale, might be membranous (scored 01).

175. Setae with long apical tube: 0. Absent. 1. Present. In *Lygromma* the tarsal tips of legs and palp bear a few setae with an elongated, pore-bearing tube (figs. 40H, 81B). See also character 270.

176. Trichobothria proximal and distal plate limit: 0. Well differentiated. The distal margin of the trichobothrial hood is well defined, often overhanging the distal plate and the opening of the socket (figs. 94N, 96D). In some cases the margin is well marked, although not overhanging (fig. 96C). 1. Not well differentiated. The distal margin of the hood is tenuous, superficial, not well marked (fig. 94D, H, M). See also next character. 2. Homogeneous. The bothrium is smooth, without distinction into proximal and distal plates (fig. 95C, E). States are ordered, as state 1 is intermediate between states 0 and 2. COMMENTS: *Hortipes*: scored from normal trichobothria, not from the modified metatarsal structure (scored 0). Cf. Gnaphosoidea TEX: from cymbium (scored 0). *Griswoldia*: from *G. robusta* (Griswold, 1991: fig: 30) (scored 0). *Philodromus*, *Tibellus*, *Petrichus*: well differentiated, but transverse ridges distal to proximal plate limit (scored 0). *Titanebo*: not clear what is the proximal plate limit, there may be transverse ridges distal to it (scored 01). *Polybetes*: more or less defined, but not well defined in the smaller trichobothria (scored 01). *Eusparassus*: variable (scored 01).

177. Trichobothria proximal and distal plates medial differentiation: 0. Hood entire, differentiated (figs. 94N, 96D). 1. Hood not differentiated medially. The distal margin of the hood is only marked at the sides (fig. 96A, B). This character was scored uncertain when the distal margin is depressed, joining the hole of the bothrium (e.g., fig. 94K). This character is applicable only when hood is well defined (char. 176, state 0). COMMENTS: *Calacadia*: sunken in the middle, at hole margin (scored ?). *Ciniflella* BRA: margin joining hole (scored 01).

178. Trichobothria proximal plate transverse ridges: 0. Smooth. The hood is smooth, without definite transverse ridges; it may have similar sculpture as the surrounding cuticle (figs. 94G, 95J). 1. With transverse ridges. The hood has well-defined transverse ridges (figs. 94O, 96E, K). These ridges are much larger than the sculpture of the surrounding cuticle (e.g., larger than the longitudinal fingerprintlike sculpture in fig. 94O). Some terminals had intermediate or ambiguous conditions (fig. 94M). COMMENTS: *Hypochilus*, *Stegodyphus*, *Uloborus*, *Megadictyna*, *Titanoeca*: from Griswold et al. (2005: figs. 154–156). *Filistata*: hood not defined, but entire area is smooth (from Griswold et al., 2005: fig. 154B) (scored 0). *Thaida*: from Forster et al. (1987: figs. 103, 104) (scored 0). *Ariadna*: intermediate (scored

01). *Araneus*: distal area smooth (scored 0). *Eresus*: very shallow undulations (scored 01). *Homalonychus*: ambiguous (scored 01). *Vectius*: very weak transverse waves (scored 01). *Ammoxenus*: concentric ridges (fig. 96K), diffuse in other preparations (scored 1). *Amaurobioides*: thin transverse ridge (scored 1). *Cheiramiona*: ambiguous and variable (scored 01). *Zora*, *Xenoctenus*, *Liocranoides*: thin longitudinal lines plus weak transverse ridges (scored 1). *Selenops*: ambiguous (fig. 94M) (scored 01). *Polybetes, Eusparassus*: very shallow ridges (scored 01). *Cocalodes*: weak ridges (scored 1).

179. Trichobothria alveolus distal margin: 0. Entire. The margin of the alveolus is smooth (fig. 95J). 1. Notched. The distal margin of the alveolus has a well-defined notch (Forster et al., 1987: figs. 103, 105), except in the most proximal tibial ones (Forster et al., 1987: fig. 104); here illustrated from a spiderling of *Austrochilus* (fig. 94B). Surprisingly, the salticid *Cocalodes* has a similar notch (fig. 95G). 2. Crenulate. Gradungulids have a wide depression, with a crenulated area (e.g., Forster et al., 1987: figs. 270, 299). This state is not present in this dataset. COMMENTS: *Hypochilus*: from Forster et al. (1987: fig. 377), but metatarsal trichobothria alveoli of immature notched! (fig. 94A) (scored 0). *Thaida*: Forster et al., 1987: fig. 103. Only the first tibial is unnotched (scored 1). *Cocalodes*: tarsal with notch as in Austrochilidae! (scored 1). *Plexippus*: perhaps a slight notch (scored 0).

180. Cuticular sculpture on distal trichobothrial plate: 0. Distal plate smooth (fig. 95J), at least at the margin of alveolus (fig. 96I). 1. Cuticular sculpture reaching alveolus margin (fig. 95I). This character was considered inapplicable for terminals with smooth or imbricate cuticle (see char. 100). COMMENTS: *Eresus*: surrounding area smooth (scored 0). *Titanoeca*: sculpture reaching close to the margin (Griswold et al., 2005: fig. 154I) (scored 01). *Pimus*: the longitudinal ridges (scored 1). *Psechrus*: very short space, not exposed in my SEM (scored ?). *Cycloctenus*: in some cases reaching very close to the margin (scored 01). *Titanebo*: no sculpture in tarsal cuticle (scored ?). *Borboropactus*: distal plate not delimited, but no cuticular sculpture in the area (scored 0).

181. Longitudinal cuticular sculpture on distal trichobothrial plate: 0. Transverse or smooth (fig. 94G). 1. Longitudinally ridged (fig. 94F). COMMENTS: *Hypochilus*: from Griswold et al. (2005: figs. 154–156); see also Forster et al. (1987: fig. 377) (scored 0). *Filistata*, *Stegodyphus*, *Uloborus*, *Megadictyna*, *Titanoeca*, *Dictyna*: from Griswold et al. (2005: figs. 154–156). *Thaida*: from Forster et al. (1987: figs. 103, 104) (scored 0). *Mandaneta*: weak longitudinal undulations (scored 01).

182. Trichobothria distal plate transverse ridge: 0. Absent. The distal plate is continuous with the surrounding cuticle, or slightly elevated (fig. 96O). 1. Distal plate embedded below transverse ridge. The distal plate ends below a cuticular ridge (figs. 95D, 96L). 2. Distal ridge continuous in a closed alveolus (fig. 95L, M). States are ordered, because the distal ridge (state 1) fuses with proximal plate margin to make the more derived state 2. Some gnaphosoids have an intermediate condition between states 1 and 2, where the alveolus is very wide (fig. 96H). COMMENTS: *Hypochilus*: from Griswold et al. (2005: figs. 154–156); see also Forster et al. (1987: fig. 377) (scored 1). *Thaida*: from Forster et al. (1987: figs. 103, 104) (scored 1). *Filistata*, *Stegodyphus*, *Uloborus*, *Megadictyna*, *Titanoeca*, *Dictyna*: from Griswold et al. (2005: figs. 154–156). *Calacadia*: no definite distal plate, the ridges from the cuticle passing over, perhaps new character (scored 0). *Paccius*: tenuous in some (scored 1). *Procopius*: borders not well defined, but in general similar to the corinnid condition (scored 012). *Hortipes*, *Cithaeron*: variable (scored 01). *Micaria*, *Desognaphosa*, *Lamponella*: intermediate (scored 12). *Centrothele*: ridge very well marked (scored 1). *Legendrena, Meedo*: ridge not well marked (scored 01). *Fissarena*: only weak ridge (scored 0). *Lessertina*: most with a distal transverse line, occasionally absent or connecting with the margin of the proximal plate (scored 1). *Xiruana*: variable, slightly so in some (scored 01). *Ciniflella* ARG: variable (scored 01). *Polybetes*: variable in the same tarsus (scored 01). *Boliscus*: distal ridge very elevated (fig. 95D) (scored 1). *Thomisus*: very faint ridge (scored 01).

183. Trichobothrial seta base thickness: 0. Thin (fig. 94A, C). 1. Thickened in a basal bulb (figs. 84D, 95O). COMMENTS: *Thaida*:

slightly expanded in a male palpal trichobothria (scored 01). *Borboropactus*: metatarsal trichobothria with expansion, tarsal on sensory field with bumps in a longer unexpanded area (fig. 95B) (scored 01).

184. Sculpture on basal expansion of trichobothrial seta: 0. Ridges or smooth (figs. 84D, 94I, J, 95H). These were scored together in the same state, as it seems that the sculpture is correlated with the cuticular sculpture. 1. Bumps (fig. 95N, O). The bumps are a synapomorphy of a large clade including lycosoids and dionychans, with a reversion in Sparassidae (see below, Lycosoids and the Root of Dionycha). COMMENTS: *Hypochilus*: not expanded, from Griswold et al. (2005: figs. 154–156), all smooth (scored -). *Thaida*: from immature (scored 0). *Huttonia*: smooth (scored 0). *Nicodamus*: too dirty (scored ?). *Oxyopes*: dirty or charging (scored ?). *Creugas*, *Medmassa*, *Jacaena*: no seta imaged (scored ?). *Uliodon*: expansion with pore (scored 1). *Polybetes*: weak ridges (scored 0). *Stephanopis ditissima*: dirty (scored ?). *Strophius*: bad images (scored ?).

185. Femoral trichobothria: 0. Absent. 1. Present. COMMENTS: *Dolomedes*: present on all legs (scored 1).

186. Tibia IV dorsal trichobothria length: 0. Less than 2.5 times tibial diameter. 1. Strikingly long, more than 3 times tibial diameter. This is a classical character for Theridiosomatidae (Coddington, 1986). COMMENTS: *Apostenus*: the apical trichobothria of tibia and metatarsus are very long, medially bent in an obtuse angle (scored 1). *Stephanopis ditissima*: tibial trichobothria I–II in two discrete, depressed fields (scored 0).

187. Metatarsal trichobothria number: 0. 1–2 (figs. 52F, 54H). 1. More than 2. This character was scored as state 1 if any of the metatarsi had more than two trichobothria (fig. 52G). COMMENTS: *Ariadna*: 1 (scored 0). *Uloborus*, *Dictyna*: from Griswold et al. (2005) (scored 0). *Mimetus*: from Schütt (2000) (scored 0). *Boliscus*: the first small trichobothria is claviform! (scored 0). *Cocalodes*: four in one row (scored 1).

188. Metatarsal trichobothria rows: 0. Single row. There may be more than one series, in one row (fig. 52H). 1. Two or three rows (fig. 52D, E). This character is inapplicable if there are only one or two trichobothria. COMMENTS: *Ariadna*, *Titanoeca*: only one (scored -). *Oecobius*: just one distal (scored ?). *Huttonia*, *Dictyna*: only one distal (scored ?). *Calacadia*: a lot of them (scored 1). *Cybaeodamus*: a retrolateral line as well (fig. 52D, E) (scored 1). *Psechrus*: the metatarsus is too long to decide (scored ?). *Aglaoctenus*: several series (scored 0). *Olbus*: two successive series in one row (scored 0). *Cheiramiona*, *Lauricius*, *Odo bruchi*: more than one series (scored 0). *Syspira*: three consecutive series (scored 0). *Ciniflella* BRA: on leg IV (scored 1). *Paravulsor*: more than one series, but near midline (scored 01). *Borboropactus*: short retrolateral row (scored 0). *Boliscus*: the first small trichobothria is claviform! (scored 0).

189. Tarsal trichobothria distribution: 0. All along tarsus (fig. 58D). 1. In an apical field close to tarsal organ (fig. 58C). 2. Basal field far from tarsal organ (fig. 57G). COMMENTS: *Oecobius*: no tarsal trichobothria (scored ?). *Otacilia*: on distal half, long tarsus (scored 0). *Orthobula*: only three in median sector (scored ?). *Micaria*: in the medial third (scored 0). *Neozimiris*: median third, tarsal organ apical (scored 0). Sparianthinae VEN: on distal half, but anterior to tarsal organ (scored 01). *Stephanopoides*: slightly beyond distal half (scored 0). *Boliscus*: only two (I) or one (II) trichobothria close to tarsal organ (scored 1). *Strophius*: only three trichobothria (large-small-large) (scored 1).

190. Tarsal trichobothria rows: 0. None (fig. 56D), trichobothria absent on tarsi. 1. Single row (fig. 56F). The single row is frequently staggered (fig. 56H). 2. Two or three rows (fig. 57E, F). States are ordered. In some cases it was conceivable to interpret several rows as one remarkably staggered row (fig. 56H). COMMENTS: *Oxyopes*: single row in Griswold (1993), but d 1-2-2 in my SEM, might be abnormal? (scored 2). *Brachyphaea*: many rows, on sides as well, also all leg surfaces with long setae similar to trichobothria (scored 2). *Pseudocorinna*: good to illustrate the very lateral rows (scored 2). *Jacaena*: all trichobothria on paler, slightly deeper spots (scored 2). *Lampona*: anterior legs with very short trichobothria (scored 2). *Pseudolampona*: two rows, restricted to anterior half (scored 2). *Ammoxenus*: more than one, but tarsus too long to see rows (scored 12). *Cithaeron*: contra Platnick (1991) (scored 2). *Malenella*: only two on the median line (scored 1). Eutichuridae MAD: two consecutive series on the median line (scored 1). Sparianthinae VEN: perhaps a case of a very staggered single row (fig. 56I) (scored 12). *Thomisus*: three trichobothria (scored 1). *Holcolaetis*: staggered on IV (fig. 56H) (scored 1).

191. Coxal gland duct: 0. Convoluted. 1. Simple. See Griswold et al. (2005: char. 53). COMMENTS: *Hypochilus*: from Marples (1968) (scored 0). *Filistata*: after *Kukulcania hibernalis* from Buxton (1913) (scored 1). *Thaida*: after *Austrochilus* from Marples (1968) (scored 1). *Ariadna*: only *Dysdera* mentioned in Buxton (1913) (scored ?). *Araneus*: after *Araneus trifolium* from Buxton (1913) (scored 1). *Ammoxenus*: from Petrunkevitch (1933) (scored 1).

192. Heart ostia: 0. Four pairs. 1. Three pairs. 2. Two pairs or less. See Griswold et al. (2005: char. 58). States are ordered, as it seems clear that the posteriormost ostia are the ones that are lost (Petrunkevitch, 1933). COMMENTS: *Hypochilus*: Petrunkevitch (1933) and Millot (1936) (scored 0). *Filistata*: after *Kukulcania hibernalis* from Petrunkevitch (1933) and L. Nieto (in litt.) (scored 1). *Thaida*: after *Austrochilus* from (Marples, 1968) (scored 0). *Ariadna*: from Petrunkevitch (1933: fig. 8) (scored 2). *Eresus*, *Uloborus*: from Petrunkevitch (1933) and Millot (1936) (scored 1). *Oecobius*, *Mimetus*, *Dictyna*, *Desis*, *Homalonychus*, *Psechrus*, *Zoropsis*, *Acanthoctenus*, *Oxyopes*, *Dolomedes*, *Ammoxenus*, *Tibellus*, *Heteropoda*, *Aphantochilus*: from Petrunkevitch (1933) (scored 1). *Araneus*: after several araneoid representatives from Petrunkevitch (1933) and Millot (1936) (scored 1). *Eriauchenius*: from Petrunkevitch (1933) (scored 12). *Nicodamus*: from Harvey (1995) (scored 1). *Ctenus*: after *C. malvernensis* from Petrunkevitch (1933) (scored 1). *Clubiona*: after a congeneric from Petrunkevitch (1933) (scored 1). *Elaver*: after *E. pallens* from Petrunkevitch (1933) (scored 1). *Castianeira*: after *C. descripta* from Petrunkevitch (1933) (scored 1). *Gnaphosa*: after *G. muscorum* from Petrunkevitch (1933) (scored 1). *Prodidomus*: after *P. amaranthinus* from Petrunkevitch (1933) (scored 2). *Anyphaena*: after *A. celer* from Petrunkevitch (1933) (scored 2). *Cheiracanthium*: after *C. mildei* and *C. erraticum* from Causard (1896) and Petrunkevitch (1933) (scored 1). *Teminius*: after *T. hirsutus* from Petrunkevitch (1933) (scored 1). *Philodromus*: after *P. vulgaris* from Petrunkevitch (1933) (scored 1). *Selenops*: after *S. insularis* from Petrunkevitch (1933) (scored 1). *Xysticus*: after *X. kochii* from Petrunkevitch (1933) (scored 1). *Lyssomanes*: after *L. portoricencis* from Petrunkevitch (1933) (scored 1).

193. Origin of dorsal dilator muscle M1 of pharynx: 0. From carapace. 1. From rostrum. See Griswold et al. (2005: char. 55). COMMENTS: *Hypochilus*: from Marples (1968, 1983) (scored 1). *Filistata*: After "*Filistata*" from Marples (1983), also "Filistatidae" in Marples (1968). The M1 is absent, only the anterior M2 muscle is present, from carapace (1983: fig. 9) (scored -). *Thaida*: From Marples (1983). Also *Austrochilus* from Marples (1968) (scored 0). *Ariadna*, *Oecobius*, *Uloborus*, *Araneus*, *Dictyna*, *Psechrus*, *Zoropsis*, *Cycloctenus*: from Marples (1983) (scored 0). *Badumna*: from Marples (1983) (sub *Ixeuticus*) (scored 0). *Cyrioctea*: *Storena* has three (Petrunkevitch, 1933) (scored ?). *Xysticus*: after *Diaea* from Marples (1983) (scored 0).

194. Fifth ventral abdominal endosternite: 0. Present. 1. Absent. See Griswold et al. (2005: char. 56). COMMENTS: *Hypochilus*: Marples (1968) (scored 0). *Filistata*: Millot (1936) (scored 1). *Thaida*: after *Austrochilus* from Marples (1968) (scored 1). *Ariadna*: after *Segestria* from Millot (1936) (scored 1). *Eresus, Uloborus*: from Millot (1936) (scored 1). *Araneus*: after *Tetragnatha* from Millot (1936) (scored 1).

195. Third dorsoventral abdominal muscles (IX segment): 0. Present. The presence of abdominal muscles was often inferred from the dorsal sclerotized patches, marking the muscle insertions (fig. 101E). When these markings are absent, and there are no direct observations or previous reports of the muscles, the scoring is left as missing. 1. Absent. See Griswold et al. (2005: char. 59). COMMENTS: *Hypochilus*: From Petrunkevitch (1933) and Marples (1968). See discussion of difference between *Ectatosticta* and *Hypochilus* in Marples (1968: 22) (scored 0). *Filistata*: from Millot (1936) (scored 0). *Thaida*: after *Austrochilus* from Marples (1968) and personal observation (scored 0). *Ariadna*: there are no dorsal markings; also after *Segestria* from Millot (1936) (scored 1). *Eresus, Araneus*: from Millot (1936) (scored 0). *Stegodyphus,* cf. *Medmassa* THA, *Eilica*, *Apodrassodes*, *Stephanopoides*: from dorsal muscle insertions (scored 0). *Huttonia*: probably reduced, no visible muscle insertions (scored ?). *Dictyna*: from dorsal markings, also after unspecified dictynid in Millot (1936) (scored 0). *Psechrus*: from Crome (1955) (scored 0).

196. Midgut diverticula in chelicerae: 0. Absent. 1. Present. See Griswold et al. (2005: char. 54). COMMENTS: *Filistata*, *Eresus*, *Oecobius*, *Uloborus*, *Araneus*, *Dictyna*, *Zoropsis*: from Millot (1931b) (scored 1). *Thaida*: after *Austrochilus* from Marples (1968) (scored 1). *Ariadna*: after *Segestria* from Millot (1931a) (scored 1).

197. Intestine profile: 0. M-shaped. 1. Straight or only slightly curved. See Griswold et al. (2005: char. 57). Haplogynae with globose abdomen (*Scytodes*, *Physocyclus*) observed by Millot (1933b: 228), do not have M-shaped intestines, only curved. Millot generalized the condition "straight" (including curved) to Araneomorphae except Hypochilidae, without specifying representatives. Millot (1931b: 740) notes that the study of the abdominal intestine is extremely difficult. Some scorings here were implied from Millot (1936, 1938, 1949). COMMENTS: *Hypochilus*: M-shaped in *Ectatosticta* (Millot, 1933b: fig. 2). *Hypochilus* has a much more attenuate, almost straight intestine (Marples, 1967: fig. 4b) (scored 1). *Filistata*: Marples (1968) remarked that the intestine in *Filistata* and *Segestria* was well defined, instead of diffuse. Here coded from sections made by L. Nieto (in litt.) (scored 0). *Thaida*: after *Austrochilus* (Marples, 1968) (scored 0). *Ariadna*: after *Segestria* from Marples (1968) (scored 1). *Eresus*: supposed from Millot (1936) (scored 1). *Oecobius*: supposed from Millot (1938) (scored 1). *Uloborus*: supposed from Millot (1936) (scored 1). *Araneus*: after *Tetragnatha*, supposed from Millot (1936) (scored 1). *Stephanopoides*: seen while dissecting tracheae, preparation MJR-1320 (scored 1).

ABDOMEN: FIRST TO THIRD SEGMENTS

The abdominal segmentation has more clear external morphological landmarks on the ventral side. Mesothelae spiders retain the dorsal tergites, but those are lost in Opisthothelae except of Atypoidea. Remains of dorsal segmentation can be seen in recently hatched spiderlings (Millot, 1931c), even reminiscent of dorsal plates in basal Araneomorphae (fig. 97C). A generalized abdominal segment is delimited posteriorly by a ventral furrow, which extends in a pair of apodemes or entapophyses. On these apodemes insert the main dorsoventral and longitudinal segmental muscles (see Purcell, 1909, 1910). The furrows and apodemes are more clearly seen in early stages of development (fig. 97A). Across spider diversity the metameric structures (muscles, book lungs, apodemes, furrows, heart ostia, etc.) are only loosely integrated as segments. For example, anterior book lungs may be dissociated from the epigastric furrow, and the posterior tracheal spiracles may be well advanced from the posterior border of their corresponding segment.

PEDICEL: The pedicel is a narrow waist between cephalothorax and abdomen, and corresponds to the first abdominal segment. It has a regular pattern of two dorsal and one ventral sclerites, and there may be other small lateral sclerotizations in the area connecting the pedicel with the pleural area of cephalothorax. The dorsal anterior sclerite connects with the carapace. The posterior dorsal sclerite has a median convex area and one series of slit sensilla at each side, perpendicular to the body axis (fig. 98A; Barth, 2002). Internally, the areas bearing the slit sensilla are prolonged posteriorly into the abdomen as strong muscle apodemes (fig. 99A). The ventral sclerite (fig. 98B) is usually triangular with a forward-extending tip, but is rather variable in shape and degree of sclerotization.

EPIGASTRIUM: The epigastric area corresponds with the second abdominal segment, between the pedicel and the epigastric furrow (fig. 98D). This region bears the anterior book lungs, the female genitalia and the male epiandrum. Some spiders, especially araneoids, have long, smooth, presumably propriosensory setae on the anterior face of abdomen around the pedicel (the "elongated

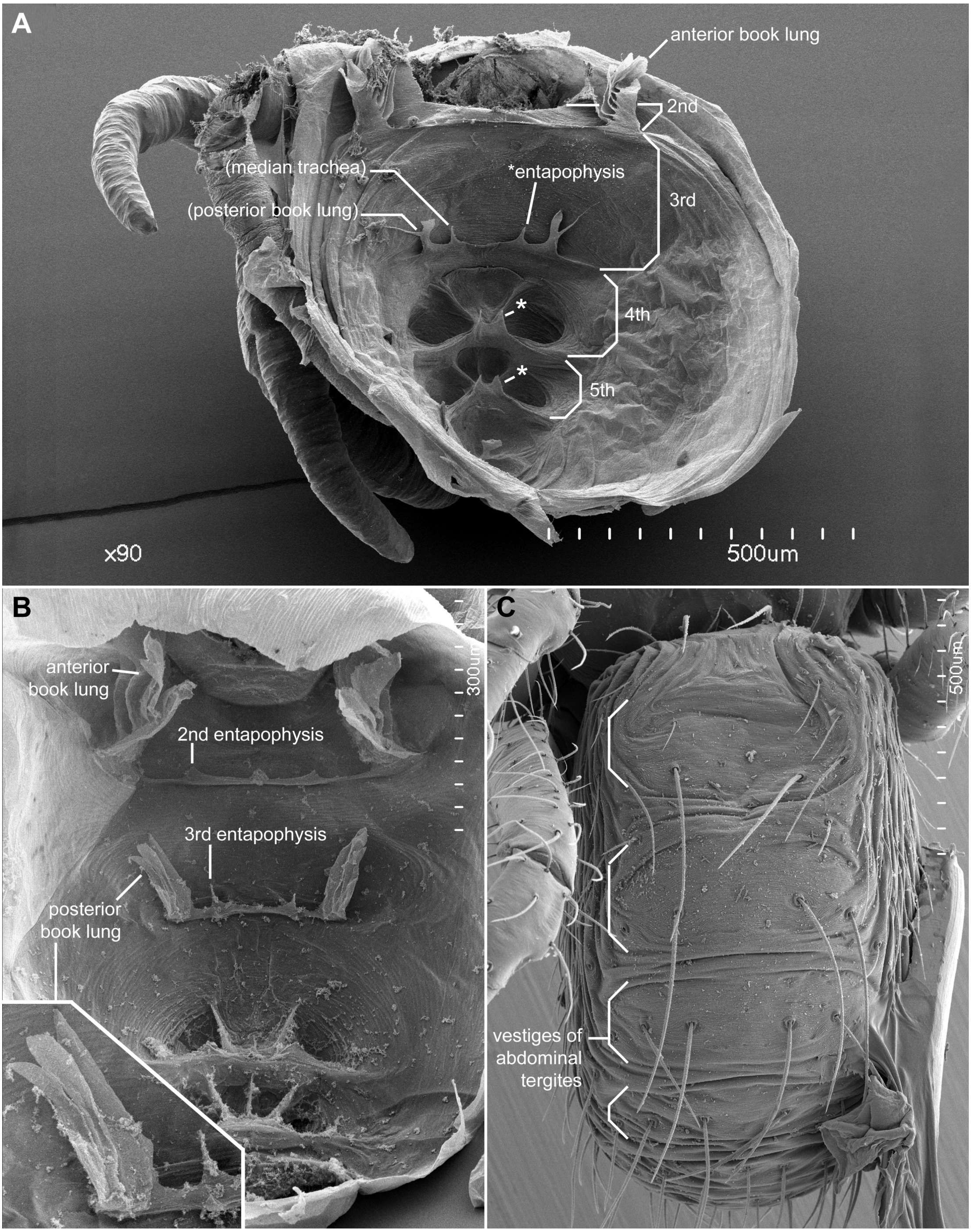

A
anterior book lung
2nd
(median trachea)
*entapophysis
3rd
(posterior book lung)
*
4th
*
5th
×90
500um
B
anterior book lung
300um
2nd entapophysis
3rd entapophysis
posterior book lung
C
500um
vestiges of abdominal tergites

Fig. 97. Segmental structures of abdomen in early spiderlings. **A.** *Thaida peculiaris* (Austrochilidae), first instar after eclosion, abdomen digested. **B.** *Filistata insidiatrix* (Filistatidae), first instar after eclosion, abdomen digested. **C.** *Ectatosticta davidi* (Hypochilidae), instar with first setae.

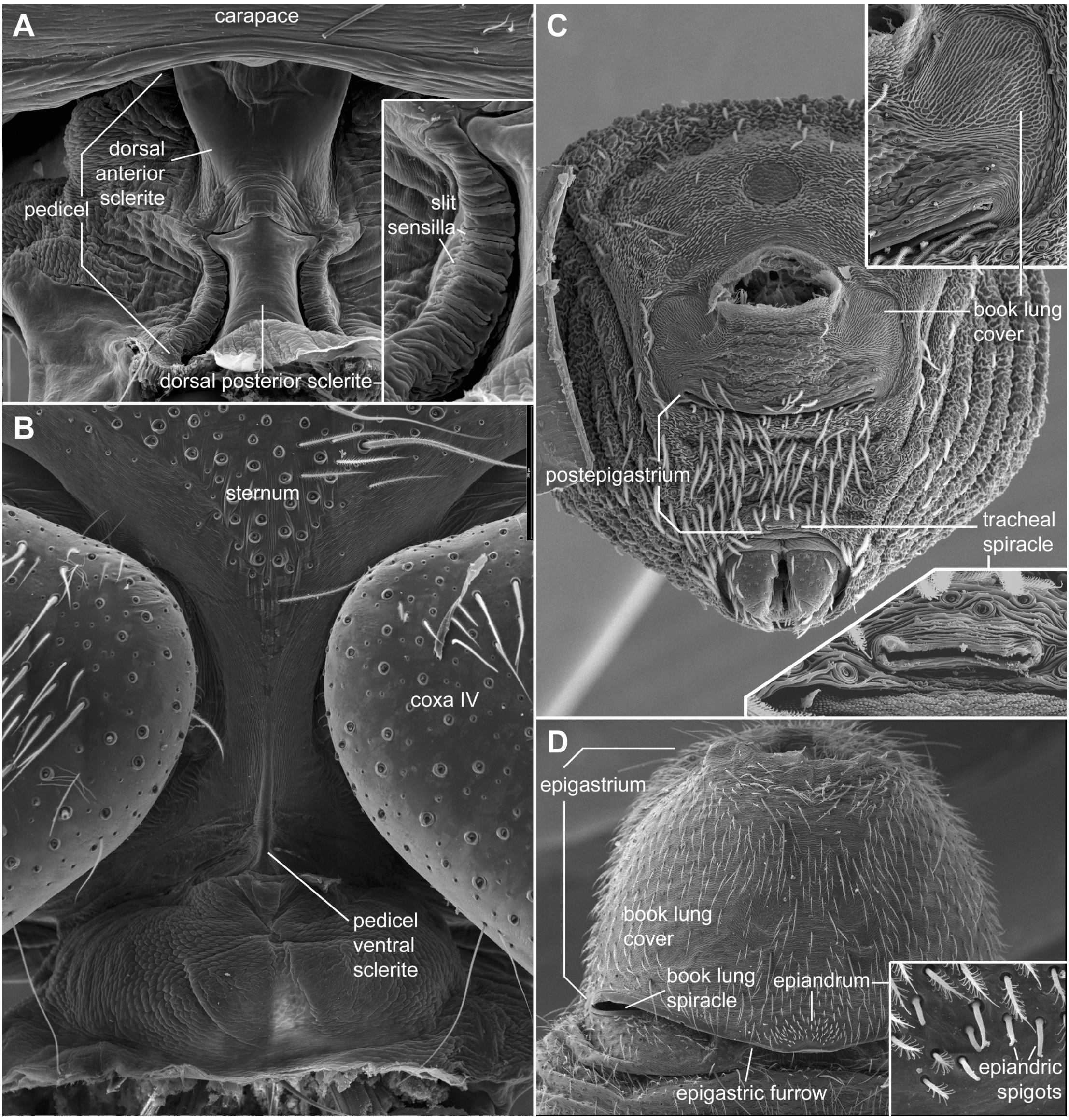

A
carapace
dorsal
anterior
sclerite
pedicel
slit
sensilla
dorsal posterior sclerite
B
sternum
coxa IV
pedicel
ventral
sclerite
C
book lung
cover
postepigastrium
tracheal
spiracle
D
epigastrium
book lung
cover
book lung
spiracle
epiandrum
epigastric furrow
epiandric
spigots

Fig. 98. Structures of abdomen. **A.** *Odo bruchi* (Miturgidae), female, pedicel dorsal. **B.** Same, ventral. **C.** *Boliscus* cf. *tuberculatus* (Thomisidae), male, abdomen ventral. **D.** *Falconina gracilis* (Corinnidae), male, epigastrium ventral.

pedicillate setae," Agnarsson et al., 2008). The male epiandrum is the area just above the epigastric furrow, corresponding to the place of the female epigyne; it frequently has several epiandric spigots (fig. 98D). The uterus externus connects the female spermathecae with the ovaries, usually inside the epigastric furrow (fig. 99A). The book lung covers are usually more sclerotized and have a different sculpture than the neighboring abdominal cuticle (fig. 98C). The book lung spiracles are usually connected with the epigastric furrow (fig. 99A). The book lungs are tracheal structures organized as flat lamellae with very thin cuticle, allowing for gas exchange. The atrium and the first

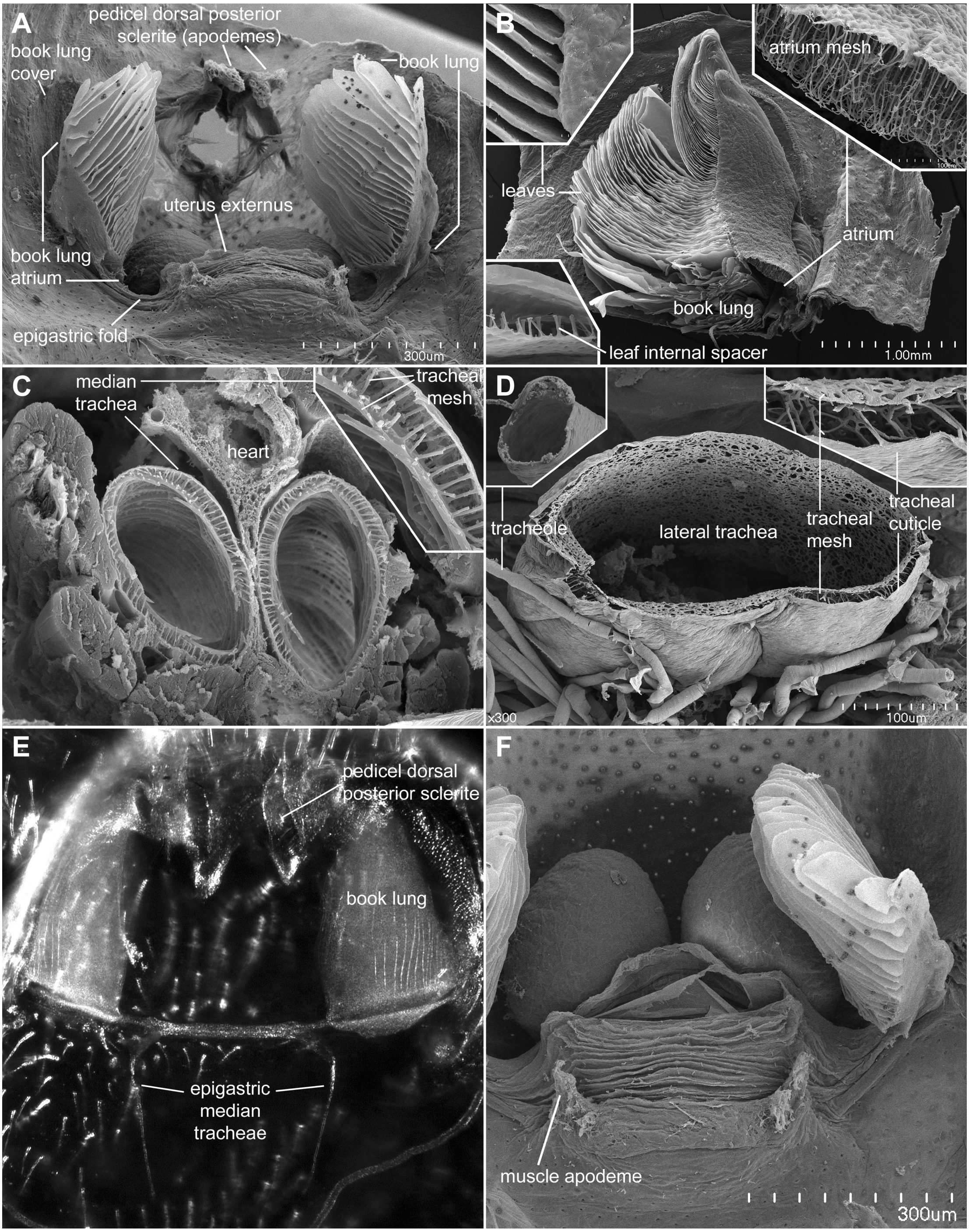

A
pedicel dorsal posterior sclerite (apodemes)
book lung cover
book lung
uterus externus
book lung atrium
epigastric fold
300um
B
atrium mesh
leaves
atrium
book lung
leaf internal spacer
1.00mm
C
median trachea
tracheal mesh
heart
D
tracheole
lateral trachea
tracheal mesh
tracheal cuticle
x300
100um
E
pedicel dorsal posterior sclerite
book lung
epigastric median tracheae
F
muscle apodeme
300um

Fig. 99. Structures of abdomen, respiratory system. **A.** *Phrurolithus festivus* (Phrurolithidae), female, book lungs. **B.** *Sicarius* sp. Tongoy (Sicariidae), female, right book lung sectioned. **C.** *Xiruana gracilipes* (Anyphaenidae), male, median tracheae, sectioned at pedicel. **D.** *Ariadna maxima* (Segestriidae), female, lateral trachea and tracheoles, sectioned. **E.** Eutichuridae MAD (Eutichuridae), subadult male, book lungs and epigastric fold showing epigastric median tracheae. **F.** *Phrurolithus festivus* (Phrurolithidae), female, book lungs and spermathecae.

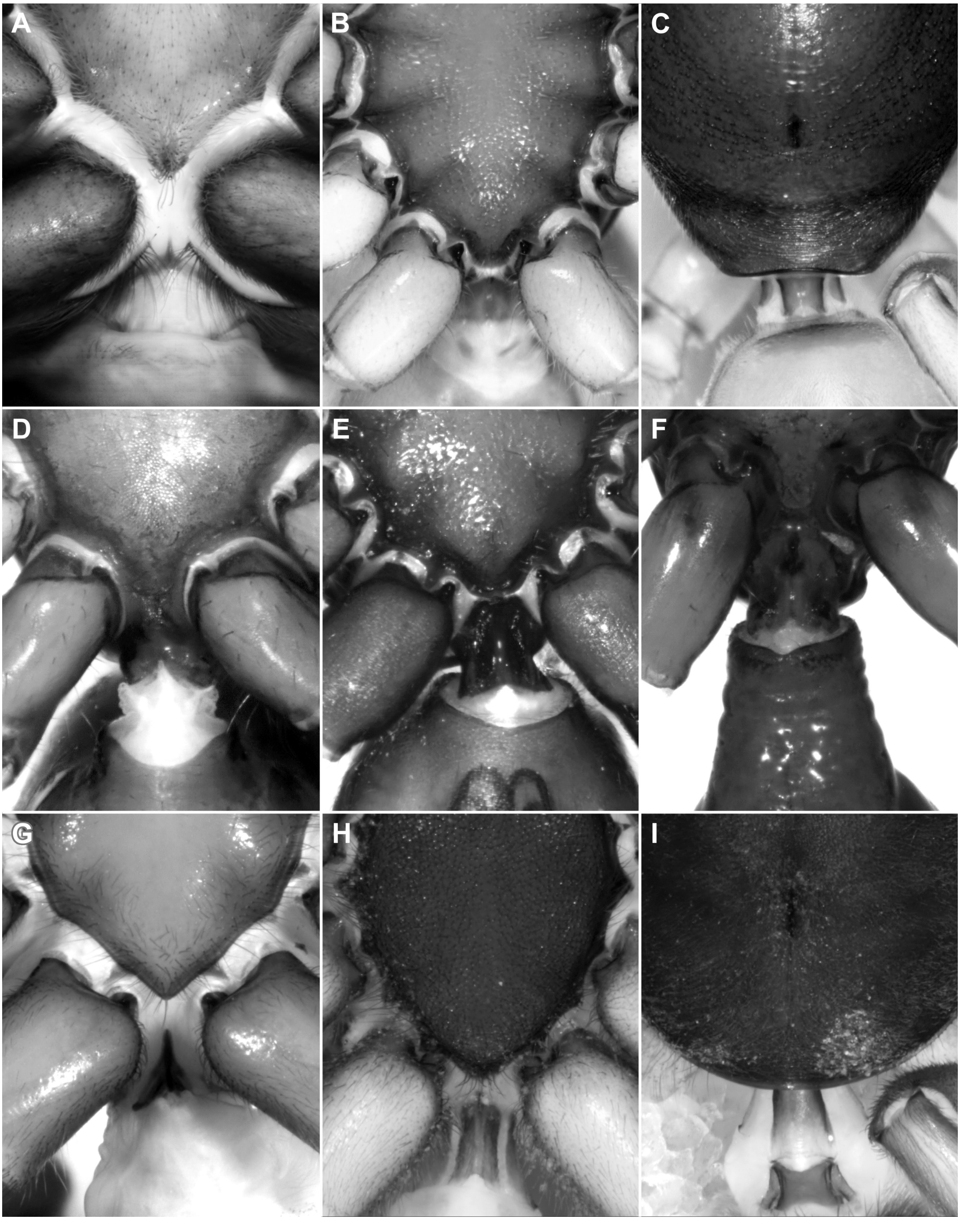


Fig. 100. Pedicel, female. **A.** *Polybetes pythagoricus* (Sparassidae). **B.** *Paccius* cf. *scharffi* (Trachelidae). **C.** Same, dorsal. **D.** *Oedignatha* sp. (Liocranidae). **E.** *Jacaena* sp. (Liocranidae). **F.** *Teutamus* sp. (Liocranidae). **G.** *Austrachelas pondoensis* (Gallieniellidae). **H.** *Lampona cylindrata* (Lamponidae). **I.** Same, dorsal.

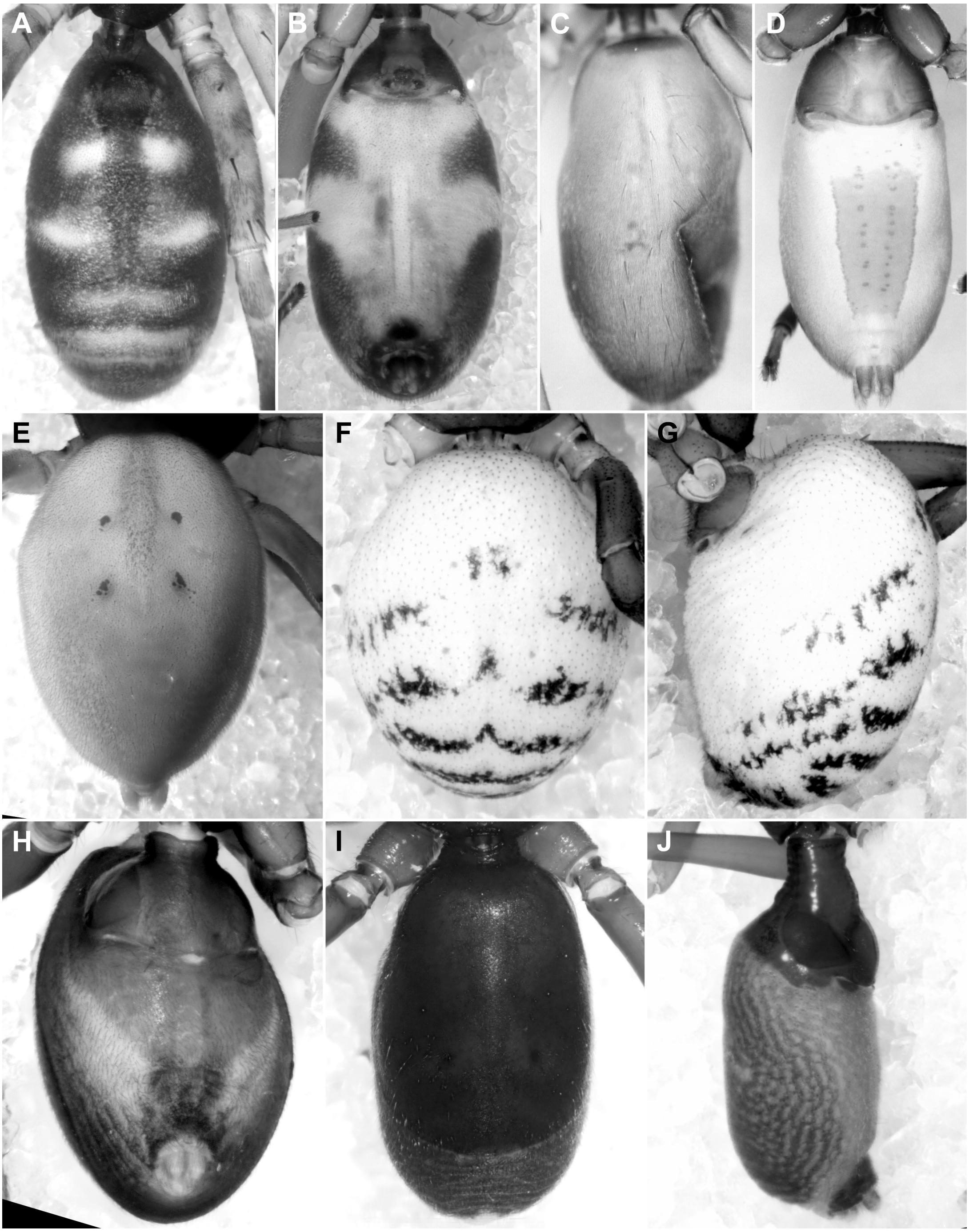


Fig. 101. Abdomen and scuta. **A.** *Castianeira* sp. Iguazu (Corinnidae), female, dorsal. **B.** Same, female, ventral. **C.** *Paccius* cf. *scharffi* (Corinnidae), female, dorsal. **D.** Same, male, ventral. **E.** *Trachelas mexicanus* (Trachelidae), female, dorsal. **F.** *Pronophaea proxima* (Corinnidae), female, dorsal. **G.** Same, female, lateral. **H.** *Oedignatha* sp. (Liocranidae), male, ventral. **I.** *Sesieutes* sp. (Liocranidae), female, dorsal. **J.** *Teutamus* sp. (Liocranidae), female, lateral.

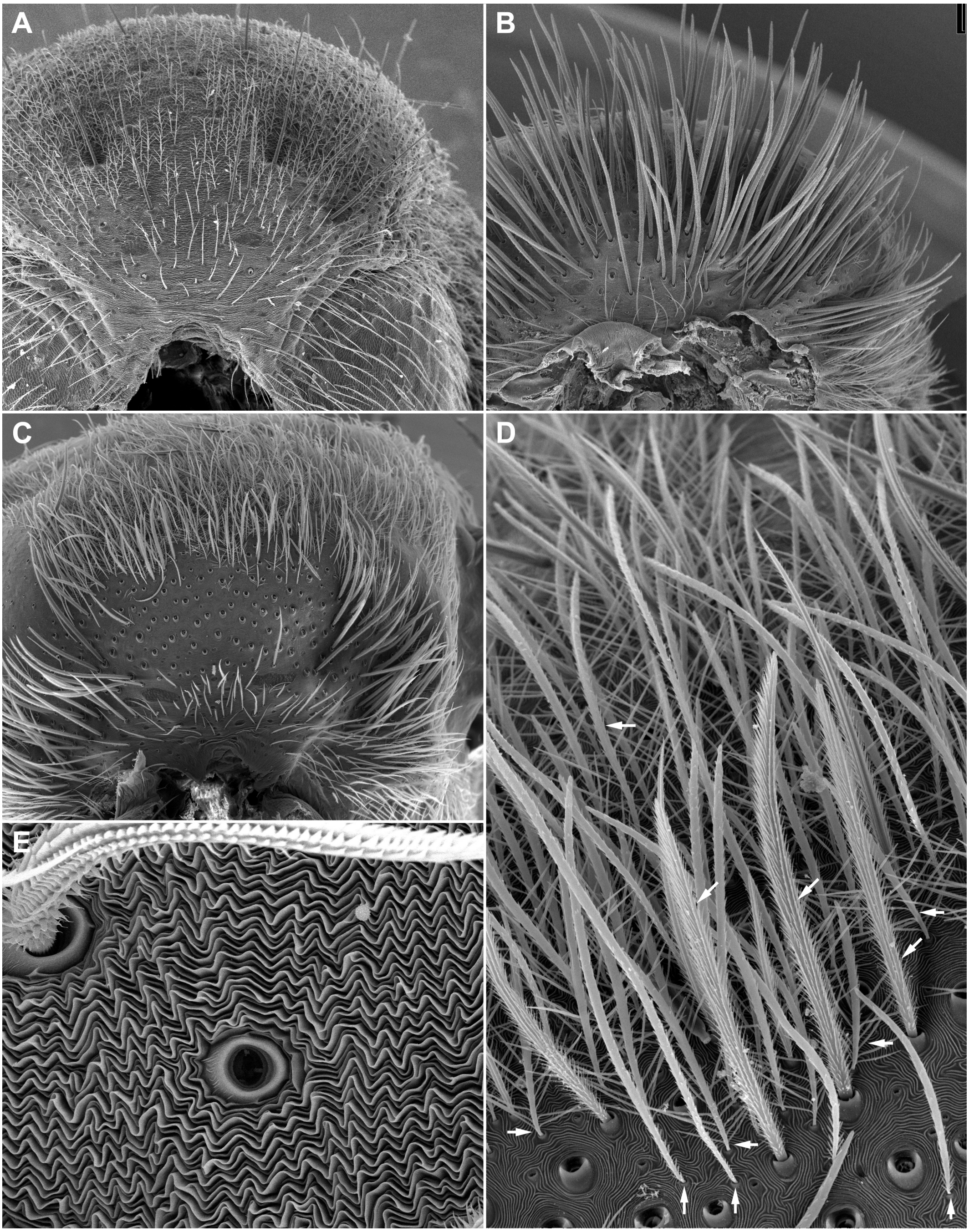


Fig. 102. Structures of abdomen. **A.** *Falconina gracilis* (Corinnidae) male, abdomen anterior dorsal area. **B.** *Apodrassodes quilpuensis* (Gnaphosidae), male, abdomen anterior dorsal area. **C.** *Odo bruchi* (Miturgidae) male, abdomen anterior dorsal area. **D.** Same, detail of anterior dorsal setae on abdomen; diagonal arrows point to strong curved setae, vertical arrows to scales without setules, horizontal arrows to scales with setules. **E.** *Cycloctenus nelsonensis* (Cycloctenidae) female, abdominal cuticle and hair socket.

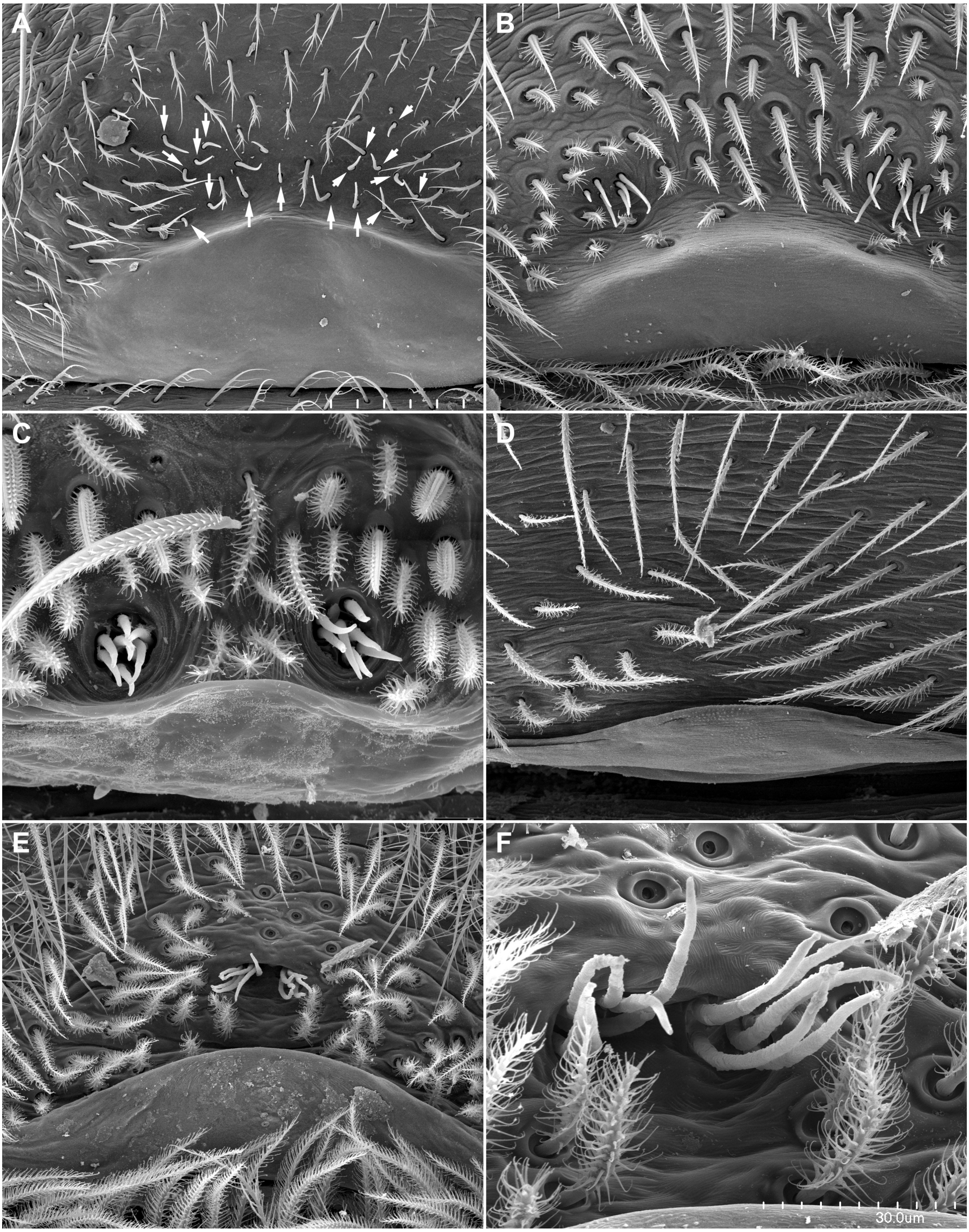


Fig. 103. Epiandrum, male. **A.** *Corinna bulbula* (Corinnidae), arrows to spigots. **B.** *Copa flavoplumosa* (Corinnidae). **C.** *Odo bruchi* (Miturgidae). **D.** *Meriola barrosi* (Trachelidae). **E.** *Lampona cylindrata* (Lamponidae). **F.** Same, detail.

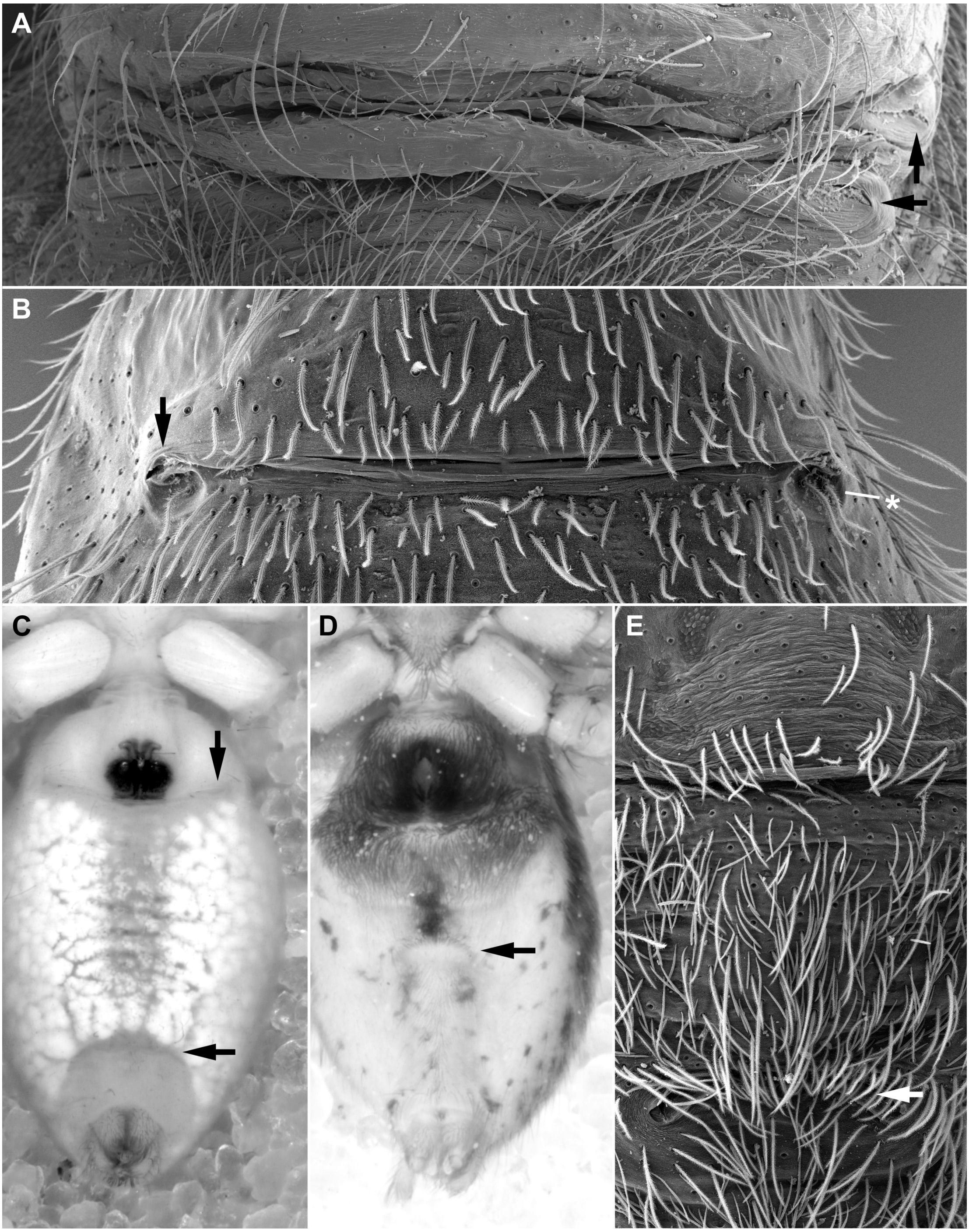


Fig. 104. Spiracles of book lungs (vertical arrows) and tracheae (horizontal arrows). **A.** *Ariadna boesenbergi* (Segestriidae) male. **B.** *Lygromma* sp. (Prodidomidae) male, showing postepigastric invaginations (asterisk). **C.** *Gayenna americana* (Anyphaenidae) female. **D.** *Anyphaena accentuata* (Anyphaenidae) female. **E.** *Xiruana gracilipes* (Anyphaenidae) male.

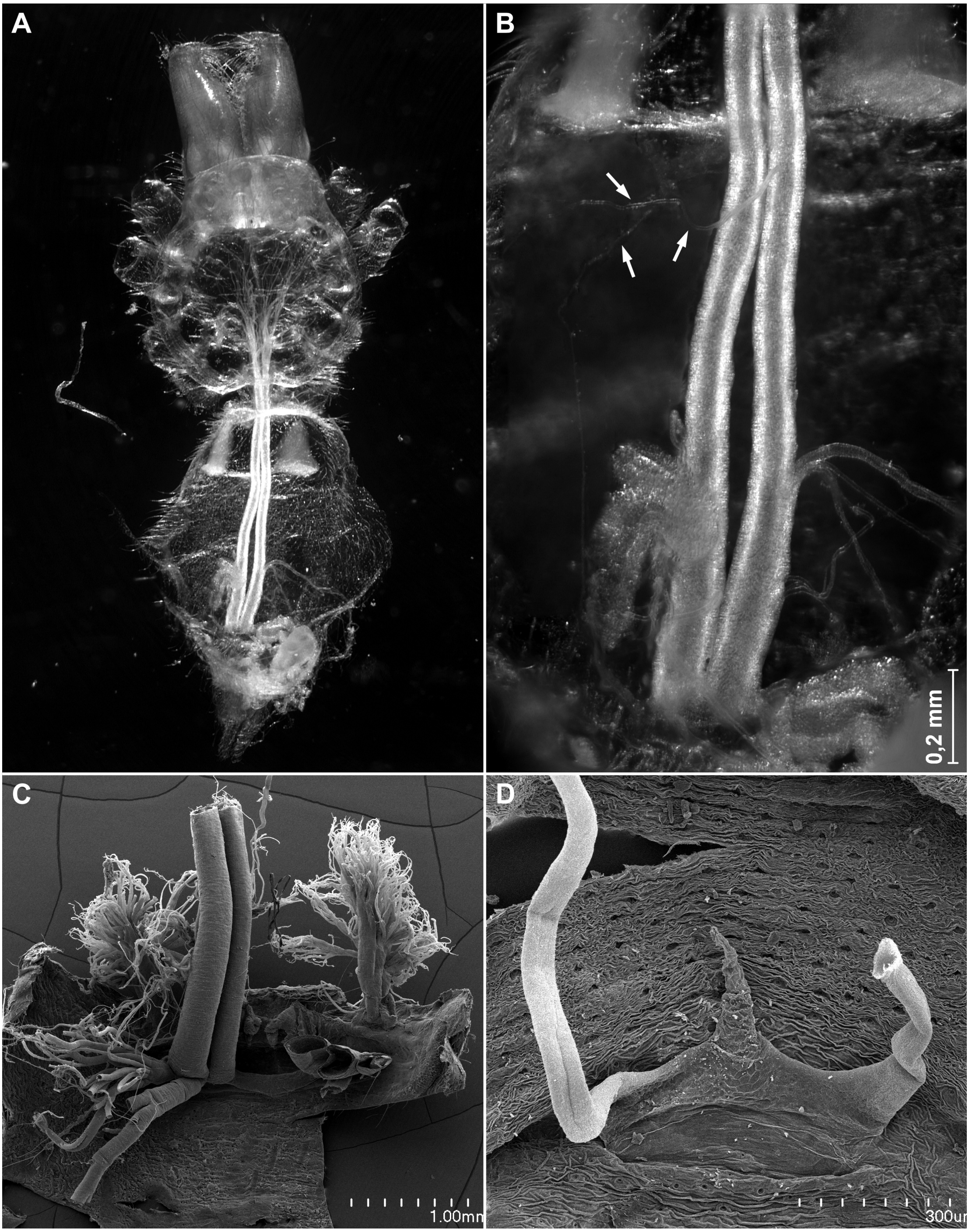


Fig. 105. Tracheal system, digested in KOH. **A.** Cf. Eutichuridae QLD (Eutichuridae?) male, dorsal view, arrows to branches of the epigastric median tracheae. **B.** Same, detail of main trunks. **C.** *Nops* sp. (Caponiidae) female, main trunks. **D.** *Scytodes intricata* (Scytodidae) female, spiracle and tracheae.

portion of each leaf are internally lined by a mesh of cuticular extensions (fig. 99B). On the leaf surface, there are hollow internal spacers arising from the ventral side, which prevent the collapsing of the air-filled leaf. Some Eutichuridae have tracheal tubes extending from the epigastric furrow, the epigastric median tracheae (fig. 99E); these seem to be extensions of the second entapophyses, similarly as occur with the median tracheae of the third segment.

POSTEPIGASTRIUM: The third abdominal segment, here referred to as postepigastrium, extends between the epigastric furrow and the spiracles of the posterior respiratory system (fig. 98C). It contains the posterior book lungs or transformations thereof. Basal Araneomorphae without posterior book lungs still preserve book lung–like structures in their early development instars (fig. 97B). The basic tracheal pattern for Entelegynae is four simple tracheae restricted to the abdomen, opening in a single spiracle near the spinnerets (fig. 98C). The median tracheae are derived from the third entapophyses, and may retain a muscle insertion at the tip; the lateral tracheae are homologous with the atrium of the posterior book lungs (Purcell, 1909). Complex tracheal systems in anyphaenids have been shown to develop from the basic system of four tubes (Ramírez, 1995); the fully developed tracheal system appears after the dispersing molt. The main tracheal trunks are lined internally by a mesh of cuticular projections, which may form an internal layer as a spiral (fig. 99C), or reticulate plate (fig. 99D). This mesh works as an open truss for the tracheal wall, while preserving the very thin tracheal cuticle needed for gas exchange. The smaller tracheoles have a simple cuticle that breaks off as a spiral thread (fig. 99D).

198. Pedicel ventral sclerite–sternum articulation: 0. Free (fig. 41A). 1. Fused (fig. 100D, F). COMMENTS: *Castianeira*: united by a thin, weakly sclerotized strip as in the precoxal or intercoxal extensions (scored 01). Cf. *Moreno* ARG: posterior end of sternum weakly sclerotized (scored 0). *Aphantochilus*: very distant, coxae IV join in between (scored 0).

199. Anterior margin of pedicel ventral sclerite: 0. Pointed (fig. 100A, G). 1. Widely truncate (fig. 100E). COMMENTS: *Ariadna*: truncated, but not widely (scored 01). *Eriauchenius*, *Trachelopachys*: narrowly truncate (scored 01). *Trachelas mexicanus*: narrow truncation, wider in some congenerics (scored 01). *Oedignatha*: pedicel ventrally fused to sternum (scored -). *Pronophaea*: slightly truncate (scored 01). *Drassinella,* cf. Gnaphosoidea TEX, *Neato*, *Tibellus*: rounded (scored ?). *Prodidomus*: pedicel and sternum close to truncate but separate (by a pilose area!) (scored 01). *Neozimiris*: hourglass shaped, not very wide (scored ?). *Galianoella*: rounded (scored 0). *Vectius*: concave (scored 1). *Platyoides*: curved, convex anteriorly (scored 1). Cf. Eutichuridae QLD: small piece, hourglass shaped, concave anteriorly (scored ?). Eutichuridae MAD: very small piece, round in front and acute posteriorly (scored ?). *Titanebo*: very small sclerotization (scored ?). *Hovops*: the area is sclerotized, without well-defined sclerite borders (scored 01). *Anyphops*: ventral sclerite only faintly sclerotized (scored ?). *Epidius*: too pale (scored ?). *Borboropactus*: area of ventral sclerite partially sclerotized, but sclerite still defined (scored 0). *Stephanopis ditissima*: area of ventral sclerite partially sclerotized, diffuse limits (scored ?). *Aphantochilus*: three anterior acute ends (scored 01).

200. Pedicel ventral sclerite forming tube: 0. Absent. 1. Present, ventral sclerite embracing dorsal (fig. 100B, C). This character is here used in a more restricted sense than in Platnick (2000). The ventral sclerite is prolonged dorsally to embrace the anterior dorsal sclerite, without fusing to it. COMMENTS: *Sesieutes*: the tube is abdominal (scored 0). *Lampona*: with lateral sclerites well separated (fig. 100H, I) (scored 0).

201. Dorsal scutum on female abdomen: 0. Absent (fig. 101G). 1. Present (fig. 101A, C, I). COMMENTS: cf. *Medmassa* THA: very small, anterior (scored 1). *Boliscus*: entire dorsum very hard in subadult female (scored 01).

202. Extension of dorsal scutum on female abdomen: 0. Small, limited to anterior half of abdomen (fig. 101A). 1. Large, extending beyond anterior half of abdomen (fig. 101I). The small scutum found in some terminals, just above the pedicel (fig. 101C) might be scored as a separate character from the more dorsal scuta. COMMENTS: *Corinna*: female has small piece above pedicel; in male same piece extends dorsally (scored 0). *Castianeira*: intermediate between a normal scutum and a small piece above pedicel (scored 0). *Paccius*: There is a small sclerotized scutum dorsal to the pedicel. The male probably has both, the small one integrated with the epigastric sclerite (scored 0). *Pseudocorinna*: just a small triangle above pedicel (scored 0). *Jacaena*: only small piece above pedicel (scored 0). *Sesieutes*: entire dorsum (scored 1). *Oedignatha*: anterior dorsal half (scored 1). *Centrothele*: small above pedicel (scored 0).

203. Female epigastric sclerite: 0. Absent, the epigastrium is soft, except for the epigyne and sometimes some patches around the book lung spiracles (fig. 167B). 1. Present, entire epigastrium sclerotized (fig. 178C). From Bosselaers and Jocqué (2002: char. 115). COMMENTS: *Mandaneta*, *Lamponella*: sclerotized on pulmonary plates and behind pulmonary spiracles, but epigynum separated by soft cuticle (scored 01).

204. Abdomen epigastric sclerite in female, extension surrounding pedicel base: 0. Absent, the sclerite is limited to the ventral surface (fig. 101F). 1. Present, the sclerite forms a closed tube surrounding the pedicel (fig. 101J) (Bosselaers and Jocqué, 2002: char. 116). COMMENTS: *Otacilia*: epigastrium sclerotized but not markedly so (scored 0).

205. Dorsal scutum on male abdomen: 0. Absent. 1. Present. From Bosselaers and Jocqué (2002: char. 102), see also Reiskind (1969: fig. 1). COMMENTS: *Medmassa*: scutum present in *M. semiaurantiaca*, but absent in South East Asian species (Deeleman-Reinhold, 2001) (scored 1). *Trachelas minor*: faint (scored 1). *Apostenus*: from Ubick and Vetter (2005) (scored 0). *Vectius*: apparently slightly sclerotized, male not well preserved (scored 01). *Legendrena*: faint anterior-central sclerotization (scored 0). *Cebrenninus*: diffusely sclerotized (scored 1).

206. Extension of dorsal scutum on male abdomen: 0. Small, limited to anterior half of abdomen. 1. Large, extending beyond anterior half of abdomen. From Bosselaers and Jocqué (2002: char. 103). COMMENTS: *Falconina*: about half the abdomen (scored 0). *Meriola*: diffuse (scored 1). *Otacilia*: anterior half (scored 01).

207. Male epigastric sclerite: 0. Absent. 1. Present. The epigastrium is sclerotized. From Bosselaers and Jocqué (2002: char. 105). COMMENTS: *Storenomorpha*: slightly more sclerotized than in female (scored 1). *Trachelas minor*: faint (scored 1). *Apostenus*: from Ubick and Vetter (2005) (scored 0). *Teutamus*: fused with the dorsal scutum (scored 1). *Pseudolampona*: just a faint, homogeneous sclerotization (scored 1). *Austrachelas*: epiandric area sclerotized (scored 0).

208. Male epigastric sclerite surrounding pedicel base: 0. Absent. 1. Present, closed tube. From Bosselaers and Jocqué (2002: char. 106). COMMENTS: *Castianeira*: fused with dorsal scutum (scored 1).

209. Ventral postepigastric scutum: 0. Absent. 1. Present in male (fig. 101D, H). I am considering here the scuta clearly posteriad of the epigatric furrow, as in Reiskind (1969). Several corinnids and lamponids have sclerotized patches just posterior to the pulmonary spiracle. Those are places of muscle insertions in many (if not all) spiders (Bosselaers and Jocqué, 2002: char. 14). This character is very variable, heterogeneous at least within *Corinna* and *Castianeira*. COMMENTS: *Pronophaea*: sclerotized patches just posterior to the pulmonary spiracle (scored 0). *Pseudolampona*: contra Platnick (2000: 303) (scored 0).

210. Female inframammillary sclerite: 0. Absent. 1. Present. A small sclerotized patch just in front of the tracheal spiracle (not in this dataset, see fig. 101B). From Bosselaers and Jocqué (2002: char. 117). COMMENTS: *Pseudoctenus*: just the spiracle protruding (scored 0). *Olbus*: both sexes with prolonged, slightly sclerotized anteror margin of tracheal spiracle (scored 0).

211. Male inframammillary sclerite: 0. Absent. 1. Present. From Bosselaers and Jocqué (2002: char. 107). COMMENTS: *Boliscus*: ring around spinnerets (scored 1).

212. Postepigastric invaginations: 0. Absent. 1. Present. These are small depressions opposing the book lung spiracles (figs. 104B, 167B). They are most often sclerotized, although the degree of sclerotization is not easily observed in pale species. This character was first proposed by Platnick (2000: char. 11) as distinctive of Lamponidae, here reported for a wider taxonomic range. COMMENTS: cf. *Medmassa* THA: present but not very deep (scored 01). *Pseudocorinna*: only the muscle attachment points (scored 1). *Sesieutes*: sclerotized plates (scored 0). *Anagraphis*: only small sclerotized plates (scored 0). Cf. Gnaphosoidea TEX: checked in digestion, the internal corners of book lung spiracle are dark (scored 0). *Syspira*: small sclerotized area from spiracle (scored 0). *Boliscus*: male with a continuous depressed transverse line (scored 0).

213. Abdomen anterior dorsal strong curved setae: 0. Present (fig. 102B–D). 1. Absent (fig. 102A). 2. Discrete macrosetae. From Bosselaers and Jocqué (2002: char. 101). COMMENTS: *Filistata*, *Eresus*, *Stegodyphus*, *Nicodamus*, *Cyrioctea*, *Cybaeodamus*, *Storenomorpha*, *Trachelopachys*, *Creugas*, *Apostenus*, cf. Gnaphosoidea TEX, *Malenella*, *Polybetes*, *Eusparassus*, Sparianthinae VEN, *Plexippus*: entire dorsum with thick setae (scored 01). *Araneus*, *Mimetus*: entire abdomen with strong but not bent setae (scored 1). *Badumna*: not a group, entire abdomen with thick setae (scored 01). *Cryptothele*: pad of short, wide, modified setae (scored ?). *Lampona*: slightly larger setae (scored 01). *Geraesta*: groups of thick setae pointing medially (scored 01). *Xysticus*, *Tmarus*, *Strophius*: macrosetae uniformly on dorsum (scored 01).

214. Epiandrous spigots: 0. Absent (fig. 103D). 1. Present (fig. 103A, B). COMMENTS: *Filistata*, *Stegodyphus*, *Oecobius*, *Uloborus*, *Mimetus*, *Dictyna*, *Badumna*, *Pimus*: from Griswold et al. (2005: figs. 157–161). *Senoculus*: contra Silva Davila (2003) (scored 0). *Aglaoctenus*: absent, but patches of setae regularly distributed (scored 1). Cf. Gnaphosoidea TEX: observed in KOH digested specimen (scored 0). *Centrothele*, *Macerio*, *Meedo*, *Austrachelas*, *Amaurobioides*: observed with stereomicroscope (scored 0). *Lamponella*: just one shaft, medial (scored 01). *Miturga* cf. *lineata*: from Silva Davila (2003) and stereomicroscope (scored 0). *Stephanopoides*: apparently absent in stereomicroscope (scored ?). *Hispo*: from SEM by Junxia Zhang (scored 0).

215. Epiandrous spigots disposition: 0. Dispersed (fig. 103A). 1. Two definite bunches (fig. 103C). COMMENTS: *Filistata, Oecobius, Uloborus, Mimetus, Dictyna, Badumna, Pimus*: from Griswold et al. (2005: figs. 157–161). *Medmassa*: almost four groups (scored 1). *Liocranum*: two spigots in one side, one in the other (scored 1). *Xenoplectus*: two, well separated (scored 1). *Eilica*: only four spigots, in two pairs (scored 01). Cf. Gnaphosoidea TEX: only two medial spigots (scored 01). *Legendrena*: two bunches not well defined, with two spigots in the middle (scored 01). *Lampona*: two definite bunches in a common pit (fig. 103E). *Lessertina*: two areas, not very definite (scored 01). *Miturga* cf. *lineata*: under the stereomicroscope can see two dense groups plus some dispersed (scored 01). *Lauricius*: two groups, but not defined bunches (scored 1). *Selenops*: two wide groups (scored 1). *Eusparassus*: in several bunches (scored 0).

216. Anterior book lungs conformation: 0. Flat leaves (fig. 99F). 1. Tubular tracheae (fig. 105C). State not represented in this dataset. COMMENTS: *Zoropsis*, *Acanthoctenus*: respiratory system from Griswold et al. (2005). *Dolomedes*: tracheae from Silva Davila (2003) (scored 0). *Clubiona*, *Elaver*: respiratory system from Silva Davila (2003) (scored 0). Cf. *Medmassa* THA: respiratory system from female maturity exuvia, decently preserved and visible (scored 0). *Trachelas mexicanus*: from *Trachelas tranquillus* (Platnick, 1974: 207) (scored 0). *Prodidomus*: small book lungs (scored 0). *Lygromma*: respiratory system from *Lygromma simoni* (in Ramírez, 1995) (scored 0). *Ammoxenus*: respiratory system from Petrunkevitch (1933) (scored 0). *Cithaeron*: narrow leaves (scored 0). *Holcolaetis*: respiratory system after *H. vellerea* from Wanless (1985) (scored 0). *Xiruana*: from Ramírez (2003) (scored 0). *Stephanopoides*: preparation MJR-1320 (scored 0). *Portia*: tracheae from Wanless (1978: fig. 1D) (scored 0). *Hispo*: respiratory system after *H. inermis* from Wanless (1981: fig. 5C) (scored 0).

217. Internal prolongations on book lung cover. 0. Absent. 1. Present. The book lung cover has internal prolongations facing the first book lung leaf. This character may be related with the report of book lung covers with pores in grate-shaped tapetum clade (L. Glatz, personal commun., in Homann, 1971: 258), "only visible in sections of old alcohol material." COMMENTS: *Thomisus*: in transverse rows (scored 1).

218. Epigastric median tracheae: 0. Absent. The epigastric furrow has internal apodemes for muscle insertion, not particularly elongated (fig. 99F). 1. Present. The muscle apodemes are remarkably elongated in thin tubes, forming a pair of tracheae (figs. 99E, 105B). A potential synapomorphy of a group of derived Eutichuridae. COMMENTS: Cf. Gnaphosoidea TEX: only two entapophyses (scored 0). *Lampona*: Platnick (2000: figs. 37–39) described these lobes as separating the postepigastric invaginations (scored 0). Cf. Eutichuridae QLD, Eutichuridae MAD: flat triangular extension extending in thin tube (scored 1). *Cheiracanthium*: in *C. inclusum* the apodemes are small, flat, rounded, projecting posteriorly, much larger in *C. punctorium* (scored 0). *Cheiramiona*: apodemes as flat triangles projecting posteriorly (scored 0). *Eutichurus*: large, round apodemes (scored 0). *Macerio*: round apodemes (scored 0). *Miturga* cf. *lineata*: like a wide central apodeme (scored 0). *Mituliodon*: apodemes small, flat, rounded, projecting posteriorly (scored 0). *Zora*: rectangular apodemes (scored 0). *Cocalodes*: dissected only below epigastric fold (scored ?).

219. Posterior book lungs or modifications: 0. Pair normal book lungs. 1. Reduced book lungs. Filistatines have reduced book lungs, with a few leaves in the hatching stage, of which only one is retained later in development (Griswold et al., 2005). Austrochilines have only one flat leaf (Ramírez, 2000). 2. Pair of tracheae (the lateral tracheae). 3. Absent (no lateral tracheae). The absence of a spiracle can be used to infer the absence of tracheae (fig. 115D). See also Ramírez (2000). COMMENTS: *Thaida*: one flat lamella (scored 1). *Filistata*: one flat lamella (scored 1). *Uloborus*: tracheae from Opell (1979) (scored 2). *Huttonia*: after *H. palpimanoides*, Forster and Platnick (1984) and personal observation (scored 2). *Megadictyna*: tracheae from Forster (1970) (scored 2). *Nicodamus*: from Forster (1970) (scored 3). *Titanoeca*, *Neoramia, Metaltella, Pimus*: tracheae from Griswold et al. (2005). *Desis*: tracheae after *D. marina* from Forster (1970) (scored 2). *Vulsor, Ctenus*: tracheae from Silva Davila (2003) (scored 2). *Cycloctenus, Toxopsiella*: tracheae from Forster and Blest (1979) (scored 2). *Teutamus*: tracheae quickly observed from immature, preparation lost during staining (scored 23). *Prodidomus*: see also *P. amaranthius* (Lamy, 1902: figs. 26, 27) (scored 2). *Legendrena*: tracheae from immature partially digested in the trap liquid (scored 2). *Neato*: not examined, but there is a small, normal tracheal spiracle (scored ?). *Trachycosmus, Desognaphosa*: no spiracle (fig. 115D). *Tibellus*: from Lamy (1902: fig. 50) (scored 2).

220. Lateral tracheae branching: 0. Simple, linear. 1. Branched. COMMENTS: *Thaida*: two "branches," the modified book lung (scored 1). *Pimus*: tracheae from Griswold et al. (2005) (scored 0). *Cheiramiona*: very long, I have cut them during dissection of abdomen (scored ?).

221. Position of openings of posterior respiratory system (or apodemes): 0. Very close to spinnerets (fig. 114E). 1. Slightly separated from spinnerets (figs. 104C, 114C). 2. Well advanced, closer to epigastrium (fig. 104A, D, E). States are ordered. COMMENTS: *Megadictyna*: only a narrow band separating from cribellum (scored 1). *Doliomalus*: about 1.5 times ALS length (scored 1).

222. Third entapophyses or median tracheae: 0. Present. 1. Absent, the internal cuticle is smooth, without prolongations for muscle insertion. See Ramírez (2000) and Griswold et al. (2005: char. 63).

223. Third entapophyses or median tracheae medially fused: 0. Separate. 1. Fused (fig. 105D). See also Ramírez (2000: char. 32). COMMENTS: *Huttonia*: one median trunk with spicles and muscle insertion (scored 1).

224. Median tracheae: 0. Absent, or only apodemes. 1. Present.

225. Median tracheae branching: 0. Unbranched. 1. Slightly branched, from two to 10 branches. 2. Strongly branched, more than 10 branches, usually hundreds of thin tracheoles. States are ordered. COMMENTS: *Neozimiris*: some branches on abdomen, main tubes pass to carapace where presumably divide (scored 2). *Cheiramiona*: two branches divide at middle of abdomen (scored 1). *Stephanopis ditissima*: flat, widened in the middle, with a short muscle insertion (scored 0).

226. Median tracheae passing to carapace: 0. Limited to abdomen. 1. Two large trunks with many ramifications passing to carapace (fig. 105A). COMMENTS: *Hortipes*: median tracheae branched after pedicel (scored 1). *Prodidomus*: two bunches (scored 1). *Thomisus*: only abdomen dissected (scored ?).

Plexippus: ramified in abdomen, and then passing through pedicel (scored 1).

227. Lateral tracheae dysderoidlike: 0. Absent. 1. Present. The large lateral tracheae have well-separated spiracles leading to large trunks suddenly splitting into many thin tracheoles (see Griswold et al., 2005: 39).

228. Spinnerets on abdominal tube: 0. Absent (fig. 114E). 1. Present. Just in front of the tracheal spriacle the abdominal cuticle is membranous, delimiting a short tube. This is typical of sparassids of the subfamily Sparianthinae (fig. 113A). A similar conformation has been recently reported for some Australian Zoropsidae as well (Raven and Stumkat, 2005). COMMENTS: Cf. Gnaphosoidea TEX: not well-defined tube, but constricted before spinnerets (scored 0).

ABDOMEN: FOURTH TO SIXTH SEGMENTS

The fourth and fifth segments bear the spinnerets. Similarly as in the two previous segments, the segmental entapophyses on the posterior margin of each segment can be seen more easily in early stages of development (fig. 106A). Each segment has two pairs of spinnerets, the median and the lateral spinnerets (fig. 106B, C). The anterior median spinnerets are preserved as such only in Mesothelae. They are absent in Mygalomorphae, and are transformed into the cribellum in Araneomorphae. The summary below synthetizes the main characteristics of the spinning organs in Araneomorphae.

CRIBELLUM: The cribellum has only a short article, the cribellum base, and a wide spinning field lined with minute spigots (fig. 108D). The cribellar spigots lack a base; the shafts arise directly from the cuticle. The shafts of the cribellar spigots are different from those of spigots on spinnerets, except the paracribellars (see below). Cribellar spigots appear in the stage with most setae, still inside the eggsac, and previous to the dispersing stage (fig. 108A). In some spiders, however, the first spigots to appear on the cribellum are a pair of relatively larger spigots with shaft and base similar to those on spinnerets (fig. 108C); this has been found in *Austrochilus* (Austrochilidae) and *Ectatosticta* (Hypochilidae) (personal obs.).

COLULUS: The colulus is a relic of the cribellum, as an articulate lobe (fig. 108E), or just as a patch of setae (fig. 108F).

ANTERIOR LATERAL SPINNERET: The anterior lateral spinnerets have three articles (fig. 106C, D), of which the two distals may be reduced or lost. The basal article is the largest, nearly cylindrical. The median article is a crescent-shaped incomplete ring, covering only the ectal or anterior area. The distal article is a short ring around the spinning field, and may be interrupted in the mesal area. In Araneomorphae the spinning field has two areas more or less delimited, the ampullate field (of ampullate gland spigots) and the piriform field (of piriform gland spigots). The piriform field is often crescent shaped, covering most of the spinning field. The ampullate field is a partly sclerotized sector on the mesal area, bearing the major ampullate gland spigots and associated sensilla (fig. 106E, F). These sensilla are strain detectors similar to the slit sensilla, with a dentrite ending in a pore (Gorb and Barth, 1996).

POSTERIOR MEDIAN SPINNERET: The posterior median spinnerets have a single article (fig. 106C, D). The spinning field is membranous, except for a slightly sclerotized area that may occur near the minor ampullate spigots. So far four gland spigot types are identified to occur in posterior median spinnerets (table 5) (fig. 107A).

POSTERIOR LATERAL SPINNERET: The posterior lateral spinnerets have two articles (fig. 106C). The basal article is cylindrical, usually the longest article. The distal article is usually crescent shaped, open mesally, and contains the spinning field. So far about five gland spigot types are identified to occur in posterior median spinnerets (fig. 107B, D) (table 5). Basal araneomorphs, especially web builders, usually have a functional association of three spigots forming a triad near the distal end of the spinning field (fig. 107C, E). The identity of individual spigots forming the triad seems to vary across groups (Griswold et al., 2005: 61–62).

SPIGOTS: The spigots are the outlets from which the silk is extruded. They are most often inserted on spinning fields with soft, flexible cuticle. Each spigot has a base and a tapering shaft with a pore at the tip (fig. 106E), and is supposedly homologous

TABLE 5
Characteristics of silk gland spigots

Summary of main characteristics of gland spigots in Araneomorphae. * Nubbins from aciniform spigots were sporadically reported for males of *Argiope bruennichi* (Araneidae; Müller and Westheide, 1993), some Uloboridae (Kovoor and Peters, 1988), and females of *Hogna* species (Lycosidae; Townley and Tillinghast, 2003). At least in *Hogna* the nubbins are in a very stereotyped, symmetrical location. All the detailed examination of other genera in the same families, and in many other families, shows that the nubbins are absent, thus the aciniform nubbins have very restricted occurrence (see also Townley and Tillinghast, 2009). ** Cylindrical spigots in immatures were documented in *Mimetus notius*, *Larinioides cornutus, Neoscona theisu* (Townley and Tillinghast, 2009: fig. 9, table 1; Yu and Coddington, 1989) and *Meriola barrosi* (this work, compare fig. 133G, H).

Spigot	Spinneret	Number	Multiples/ Singular	Produce nubbins	Produce tartipores	Sexual dimporphism	Heterogeneity	Size	Function
Cribellar	Cribellum	Many	Multiples	No	No	Degenerate in male	No	smallest	Cribellate mat
Major ampullate	ALS	2-several (basal Araneomorphae) 2-1 (most derived Araneomorphae)	Multiples in basal Araneomorphae and Deinopidae, singulars in the rest.	Yes, 1, posterior of 2	Yes, 1	Sometimes (male has nubbin)	Sometimes, in size and shape	Usually> Pi ≈ MiAm > Ac	Dragline, structural cables
Piriform	ALS	Many	Multiples	No	Yes	Sometimes (larger in male)	Sometimes, especially on mesal sector (e.g., Clubionidae, Pholcidae)	Usually <MaAm	Glue of attachment disc
Minor ampullate	PMS	2-1 several? (Eresidae)	Singulars	Yes, 1	Yes, 1	Sometimes (male has nubbin)	No	Usually ≈ MaAm	Dragline, structural cables
Aciniform	PMS-PLS	Many	Multiples	No *	Yes	Occasionally, in number	Perhaps (*Gradungula, Hickmania, Uroctea, Nicodamus*)	<Cy, MaAm, MiAm, MS	Wrapping, lining surfaces
Cylindrical	PMS-PLS	Many (few stereotyped in some groups)	Usually multiples, singulars in e.g., Araneoidea, some Corinnidae	No	No	Only adult females (sometimes small in immature females) **	No	> Ac	Eggsac layers, hygroregulation
Paracribellar	PMS-PLS	Many, or 2-1 as flanking of triplet	Multiples	Yes	No	Often, nubbins in male	No	≈ Ac	Fibrils in cribellate band
PLS "Modified" (= Fg)	PLS	1	Singular	Yes	No	Sometimes, nubbin in male	–	> Ac	Axis of adhesive band

TABLE 5
(Continued)

Spigot	Spinneret	Number	Multiples/ Singular	Produce nubbins	Produce tartipores	Sexual dimporphism	Heterogeneity	Size	Function
Flanking of triad	PLS	2	Singulars	Yes	No	Sometimes, nubbin in male	Not variable within species	Variable according to type	Unknown, but see Agg
Aggregate (type of flanking of triad)	PLS	2	Singulars	Yes	No	Often, nubbins in male	No	> Ac	Glue of viscid threads

with a seta. Chemosensory setae have a pore at the tip and reduced articulation with the socket, hence they seem the best candidates for spigot precursors. Spigots are named after the gland type they serve (Kovoor, 1977); to make the reading easier, spigot names are sometimes abbreviated, e.g., "piriform spigot" or "piriform" stands for "piriform gland spigot." There are several silk gland types, and in general each type is served by a morphologically distinct spigot type (Coddington, 1989). The morphology of the shaft is usually more conservative than that of the base. Some spigot types occur in small number and in stereotyped positions, and it is possible to establish homology relations for individual spigots (singulars); other spigots occur in larger number, without a precise location (multiples) (Coddington, 1989). The exact location and number of multiples is slightly asymmetrical in the same individual. Reduction and specialization of gland spigot patterns resulted in several evolutionary transformations from multiples to singulars (e.g., the mesal pair of major ampullates in most Araneomorphae, the few cylindricals of araneoids and some corinnids). Table 5 summarizes the main aspects of the external morphology, ontogeny and function of the spigot types recognized thus far, updating upon the previous accounts by Coddington (1989) and Griswold et al. (2005).

NUBBINS: Nubbins are cuticular protuberances in the spinning fields, representing "a nonfunctional, only partially formed, i.e. vestigial, spigot, either morphologically singular or multiple" (as redefined in Townley and Tillinghast, 2003: 213).

TARTIPORES: A tartipore is "a cuticular scar, morphologically singular or multiple, that results, after ecdysis, from a collared opening forming in the developing exoskeleton during proecdysis; the opening accommodates a silk gland duct, allowing the duct to remain attached to a spigot on the old exoskeleton during proecdysis" (as redefined in Townley and Tillinghast, 2003: 213). This mechanism allows the use of silk during the proecdysis, through gland ducts that pierce the forming cuticle to remain attached to the shedding spigots. The more generalized spigot types of araneomorphs (ampullates,

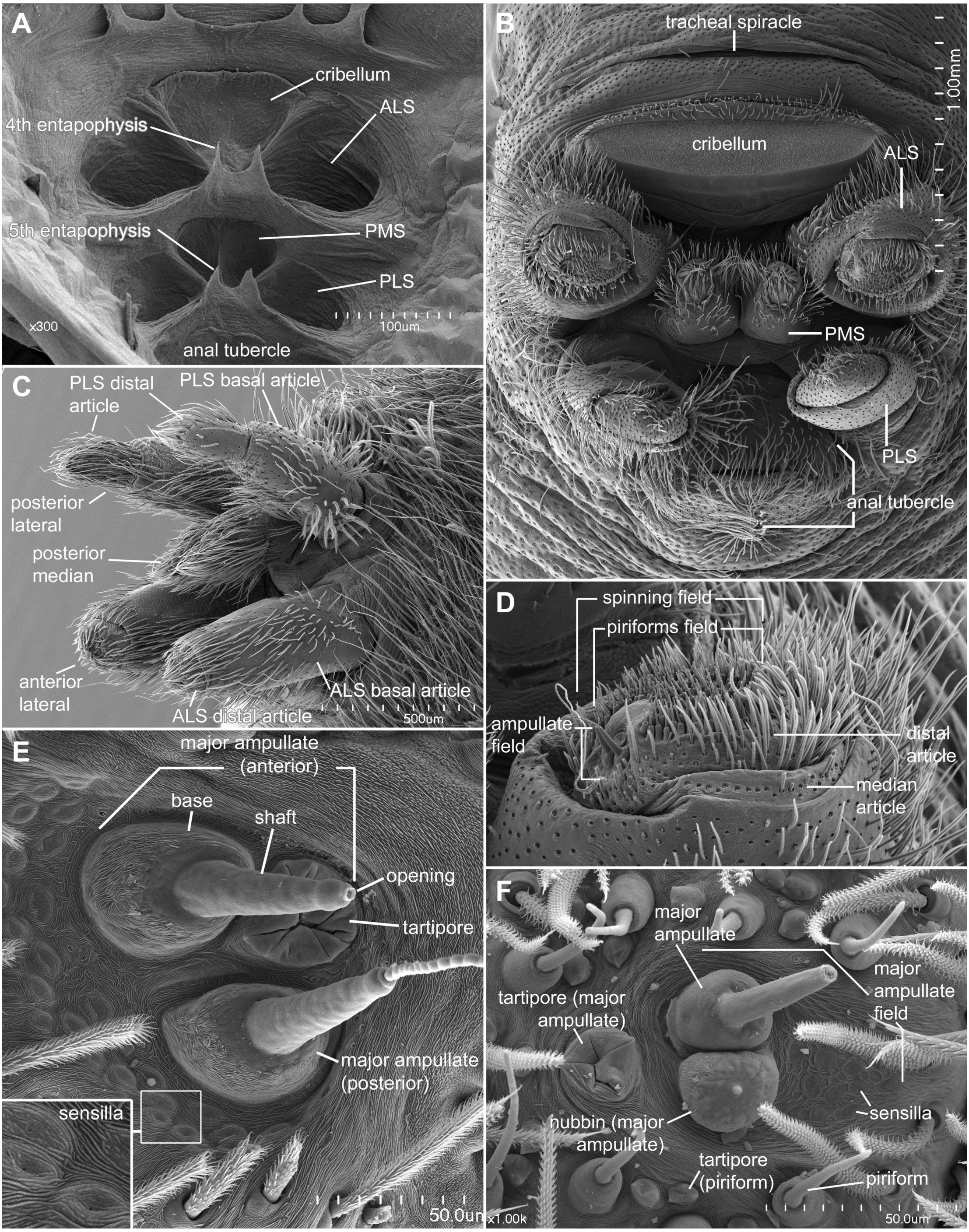

A
cribellum
ALS
4th entapophysis
5th entapophysis
PMS
PLS
x300
100um
anal tubercle
B
tracheal spiracle
1.00mm
cribellum
ALS
PMS
PLS
anal tubercle
C
PLS distal article
PLS basal article
posterior lateral
posterior median
anterior lateral
ALS basal article
ALS distal article
500um
D
spinning field
piriforms field
ampullate field
distal article
median article
E
major ampullate (anterior)
base
shaft
opening
tartipore
major ampullate (posterior)
sensilla
50.0um
F
major ampullate
major ampullate field
tartipore (major ampullate)
nubbin (major ampullate)
sensilla
tartipore (piriform)
piriform
x1.00k
50.0um

Fig. 106. Structures of spinnerets and gland spigot types. **A.** *Thaida peculiaris* (Austrochilidae) first instar after eclosion, internal view digested. **B.** Same, female. **C.** *Acanthoctenus* cf. *spinipes* (Ctenidae) female. **D.** *Thaida peculiaris* (Austrochilidae) female, right ALS. **E.** Same, detail of major ampullate field. **F.** *Uliodon* cf. *frenatus* (Zoropsidae) male, right ALS, major ampullate field.

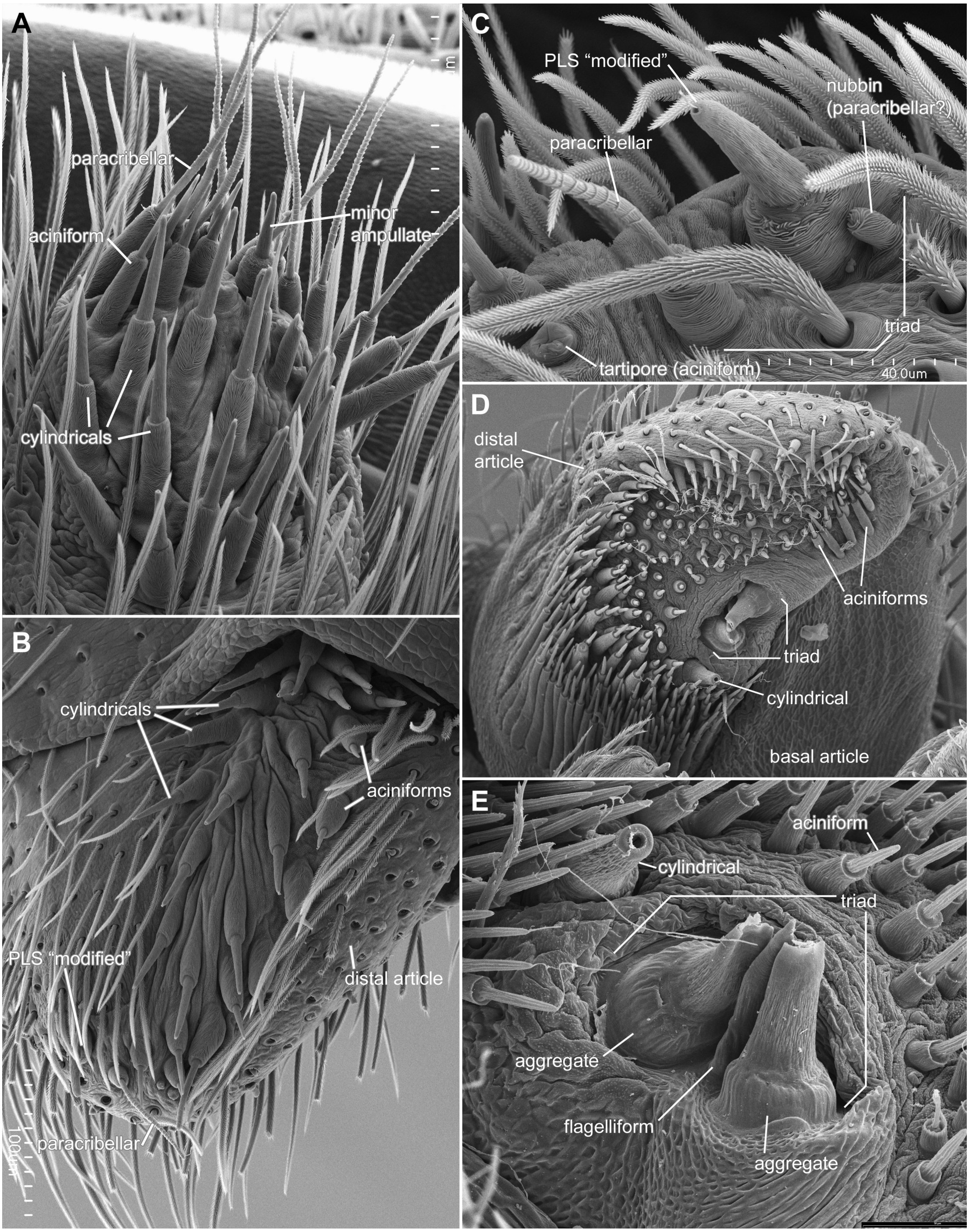

A
paracribellar
aciniform
minor ampullate
cylindricals
B
cylindricals
aciniforms
PLS "modified"
distal article
paracribellar
100um
C
PLS "modified"
nubbin (paracribellar?)
paracribellar
triad
tartipore (aciniform)
40.0um
D
distal article
aciniforms
triad
cylindrical
basal article
E
aciniform
cylindrical
triad
aggregate
flagelliform
aggregate

Fig. 107. Structures of female spinnerets and gland spigot types. **A.** *Thaida peculiaris* (Austrochilidae) right PMS, posterior. **B.** Same, right PLS. **C.** Same, left PLS triad. **D.** *Araneus* sp. (Araneidae) right PLS. **E.** Same, PLS triad.

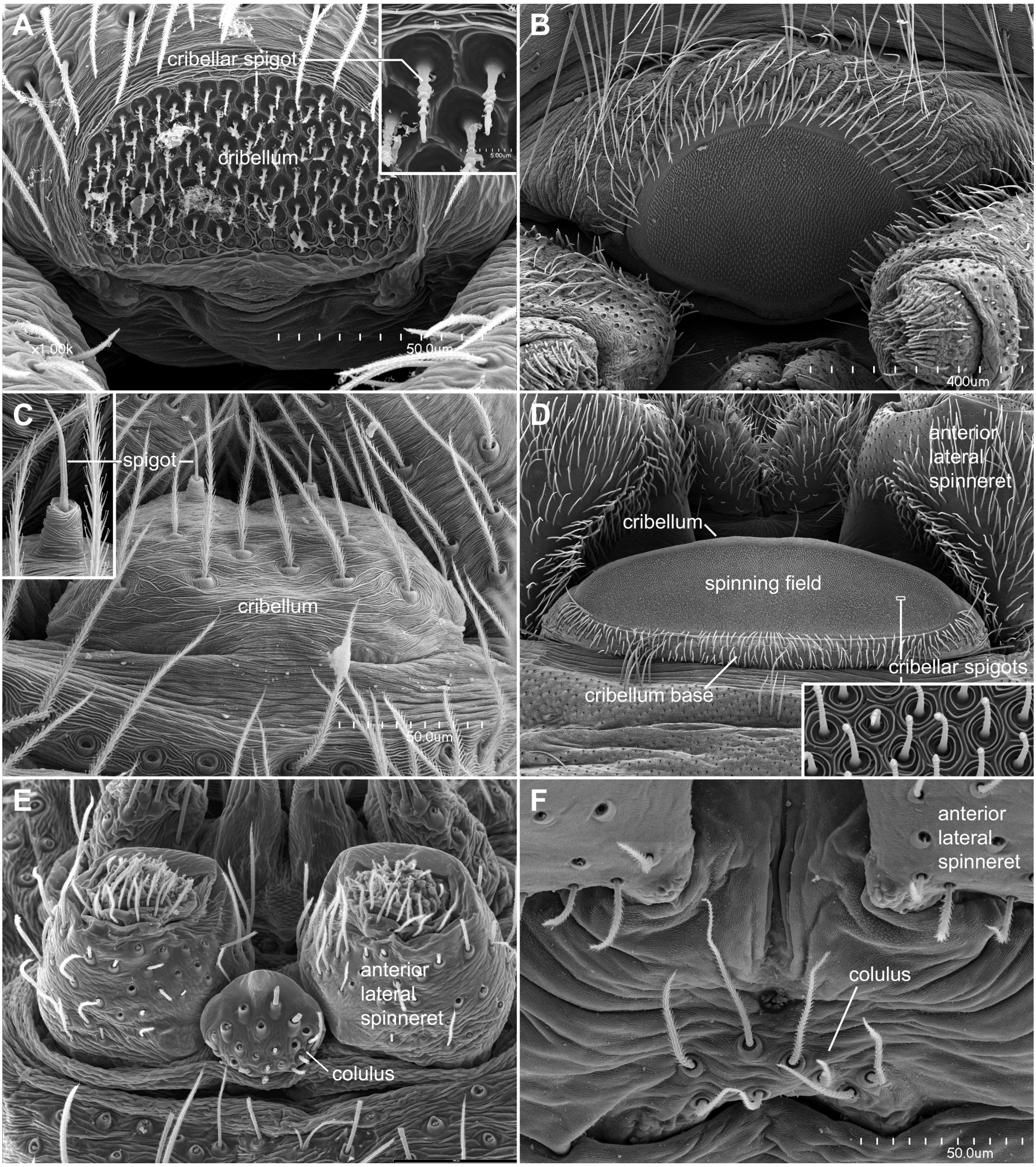

A
cribellar spigot
cribellum
5.00um
×1.00k
50.0um
B
400um
C
spigot
cribellum
50.0um
D
anterior
lateral
spinneret
cribellum
spinning field
cribellar spigots
cribellum base
E
anterior
lateral
spinneret
colulus
F
anterior
lateral
spinneret
colulus
50.0um

Fig. 108. Development and Structures of cribellum and colulus. **A.** *Hypochilus pococki* (Hypochilidae) early spiderling, stage with most hairs. **B.** Same, adult female. **C.** *Austrochilus forsteri* (Austrochilidae) early spiderling, stage with most hairs. **D.** *Thaida peculiaris* (Austrochilidae) female. **E.** *Drymusa rengan* (Drymusidae) female. **F.** *Hispo* sp. (Salticidae) female.

piriforms, aciniforms), as well as those of mygalomorphs, have corresponding tartipores; the more specialized types lack them (cribellars and paracribellars, modified and flanking spigots in the PLS triplet, cylindricals) (table 5); the Haplogynae lack tartipores.

Anal Tubercle: The six abdominal segments beyond the spinnerets are only superficially discernible in Mesothelae, and

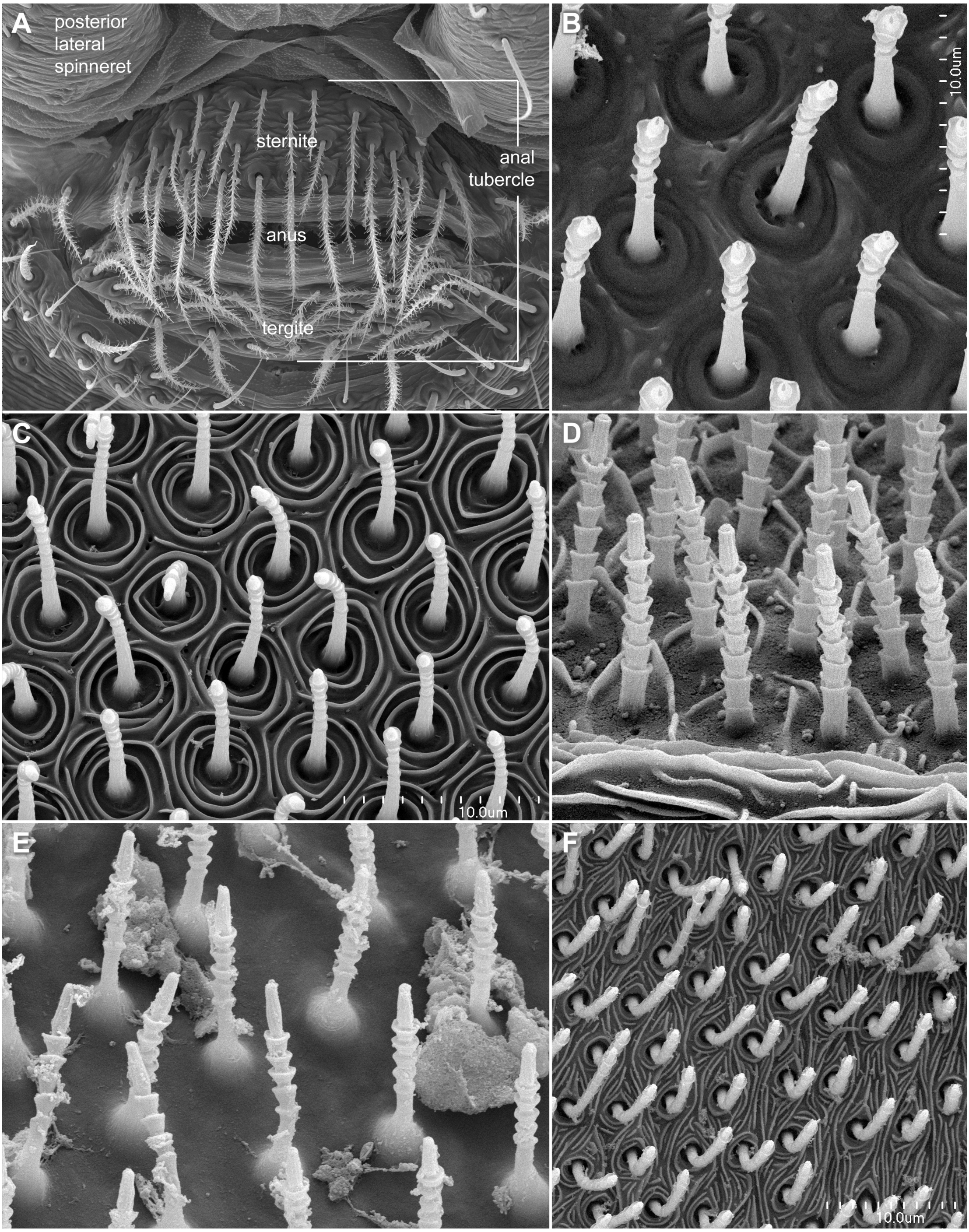

A
posterior lateral spinneret
sternite
anal tubercle
anus
tergite
B
10.0um
C
10.0um
D
E
F
10.0um

Fig. 109. Structures of anal tubercle and cribellar spigots, female. **A.** *Pronophaea proxima* (Corinnidae). **B.** *Hypochilus pococki* (Hypochilidae). **C.** *Thaida peculiaris* (Austrochilidae). **D.** *Uloborus glomosus* (Uloboridae). **E.** *Eresus* cf. *kollari* (Eresidae). **F.** *Psechrus argentatus* (Psechridae).

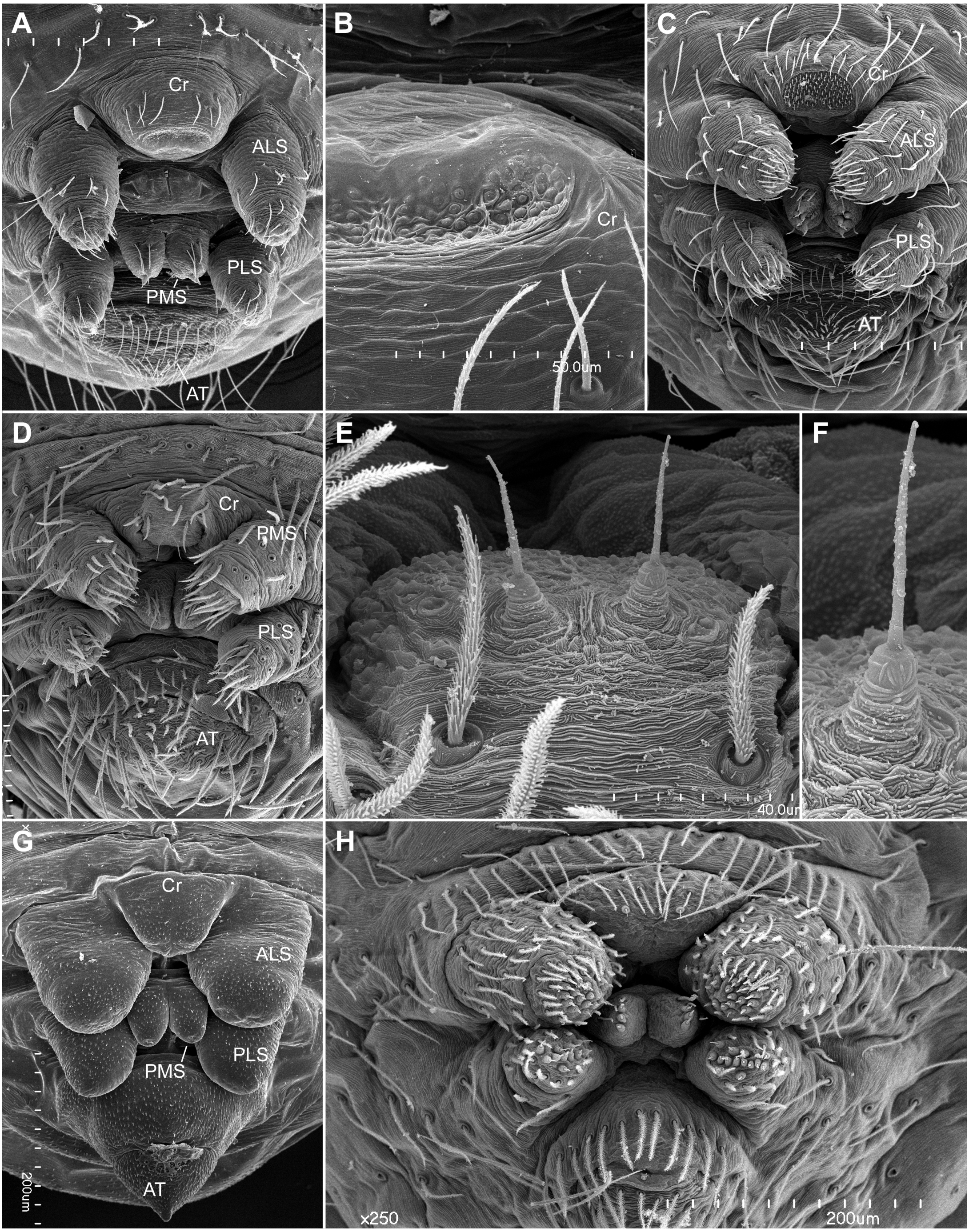

A
Cr
ALS
PLS
PMS
AT
B
Cr
50.0um
C
Cr
ALS
PLS
AT
D
Cr
PMS
PLS
AT
E
40.0um
F
G
Cr
ALS
PLS
PMS
AT
200um
H
x250
200um

Fig. 110. Development of cribellum. **A.** *Hypochilus pococki* (Hypochilidae) early spiderling, stage with few hairs, spinnerets. **B.** Same, detail of cribellum. **C.** Same, early spiderling, stage with most hairs. **D.** *Ectatosticta davidi* (Hypochilidae) early spiderling, stage with most hairs, spinnerets. **E.** Same, detail of cribellum. **F.** Same, detail of cribellar spigot. **G.** *Austrochilus forsteri* (Austrochilidae) early spiderling, stage with few hairs, spinnerets. **H.** Same, stage with most hairs.

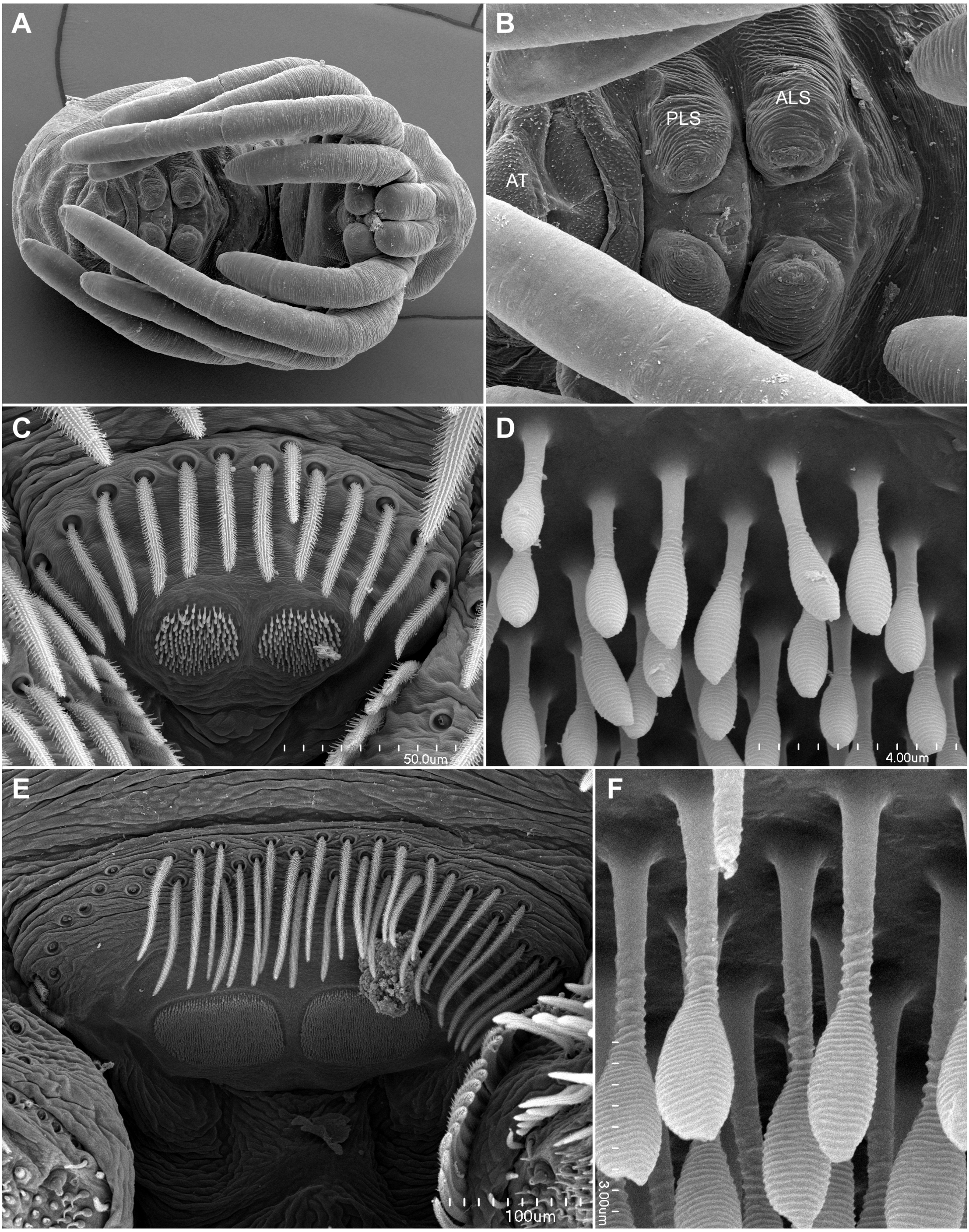

A
B
PLS
ALS
AT
C
50.0um
D
4.00um
E
100um
F
3.00um

Fig. 111. *Filistata insidiatrix*, development of cribellum. **A.** First instar after eclosion, ventral. **B.** Same, detail of spinnerets. **C.** Second instar, cribellum. **D.** Same, detail of cribellar spigots. **E.** Adult female, cribellum. **F.** Same, detail of cribellar spigots.

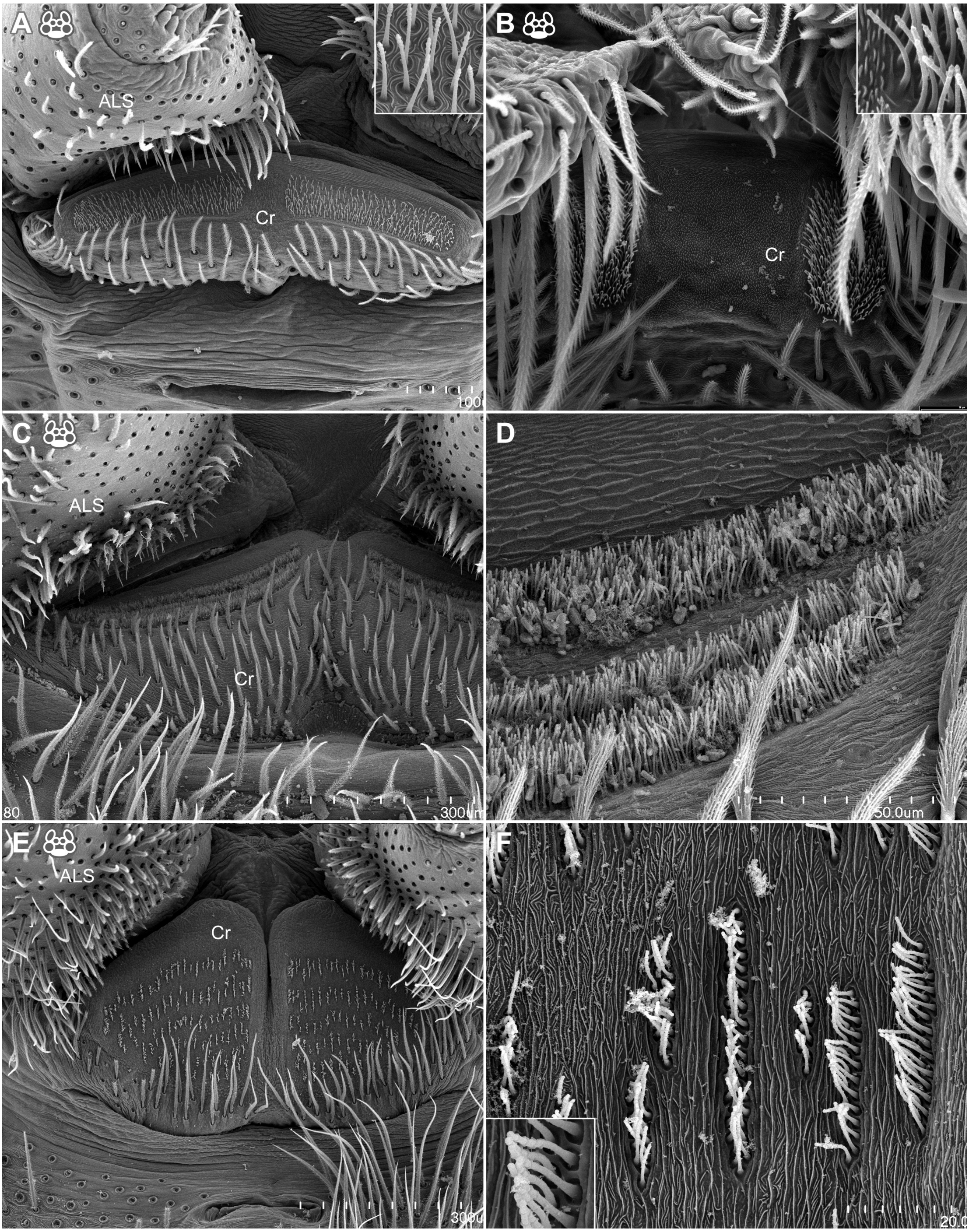

A
ALS
Cr
100
B
Cr
C
ALS
Cr
80
300u
D
50.0um
E
ALS
Cr
300
F
20.0

Fig. 112. Cribellum and cribellar spigots, female. **A.** *Pimus napa* (Amaurobiidae). **B.** *Ciniflella* ARG (Tengellidae). **C.** *Zoropsis rufipes* (Zoropsidae). **D.** Same, spigots. **E.** *Acanthoctenus* cf. *spinipes* (Ctenidae). **F.** Same, spigots.

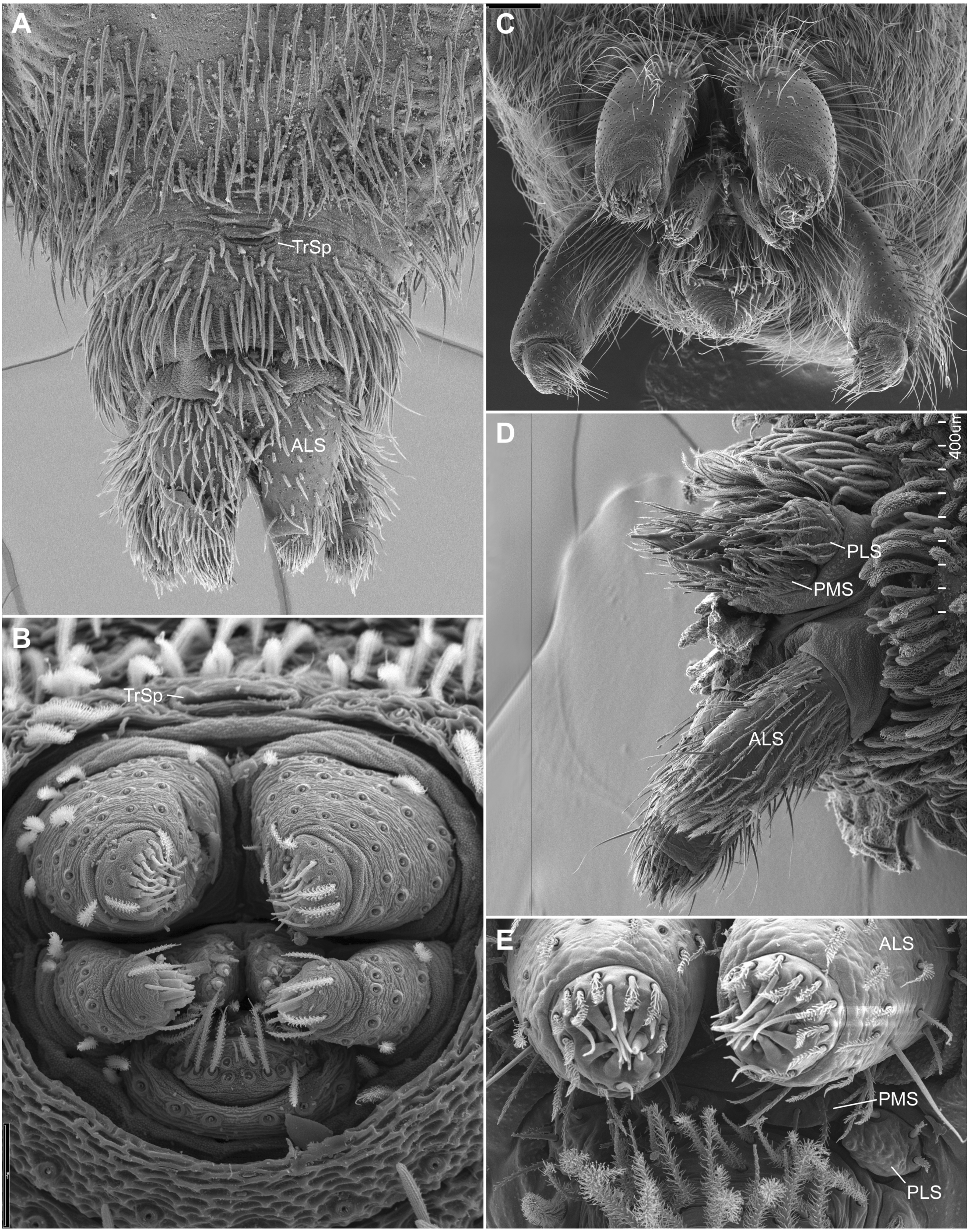

A
TrSp
ALS
B
TrSp
C
D
400um
PLS
PMS
ALS
E
ALS
PMS
PLS

Fig. 113. Spinnerets. **A.** Sparianthinae VEN (Sparassidae) female. **B.** *Boliscus* cf. *tuberculatus* (Thomisidae) male. **C.** *Eusparassus* cf. *walckenaeri* (Sparassidae) male. **D.** *Cryptothele* sp. Sri Lanka (Zodariidae) female, lateral. **E.** *Cryptothele alluaudi* (Zodariidae) immature.

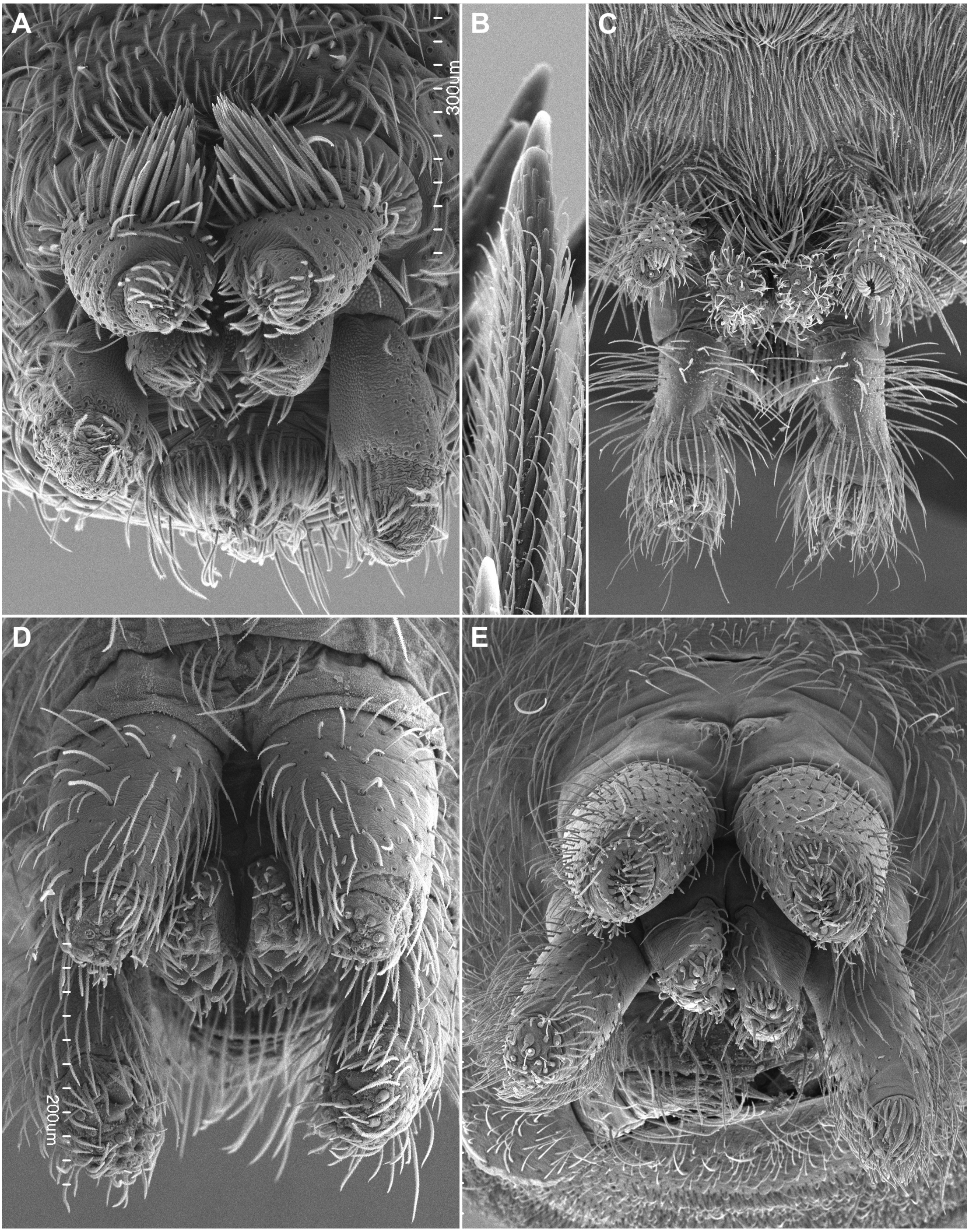


Fig. 114. Spinnerets. **A.** *Zora spinimana* (Miturgidae) male. **B.** Same, detail of thick seta on ALS. **C.** *Ammoxenus amphalodes* (Ammoxenidae) male. **D.** *Meriola barrosi* (Trachelidae) female. **E.** *Paccius* cf. *scharffi* (Trachelidae) female.

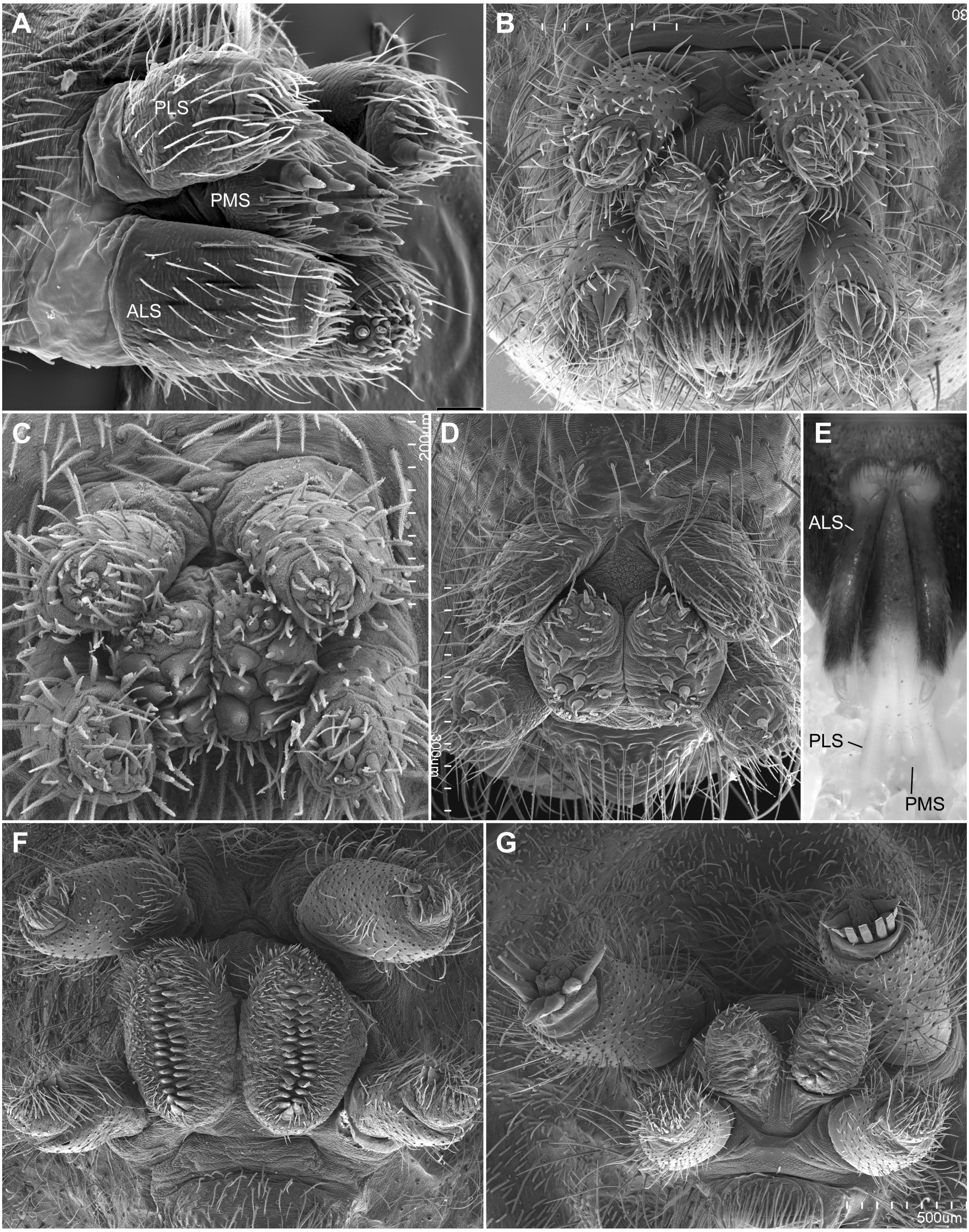

A
PLS
PMS
ALS
B
C
200um
D
300um
E
ALS
PLS
PMS
F
G
500um

Fig. 115. Spinnerets, female. **A.** *Pronophaea proxima* (Corinnidae). **B.** *Drassinella gertschi* (Phrurolithidae). **C.** *Toxoniella* sp. (Liocranidae). **D.** *Trachycosmus sculptilis* (Trochanteriidae). **E.** *Molycria stanisici* (Prodidomidae). **F.** *Fissarena castanea* (Trochanteriidae). **G.** *Gnaphosa taurica* (Gnaphosidae).

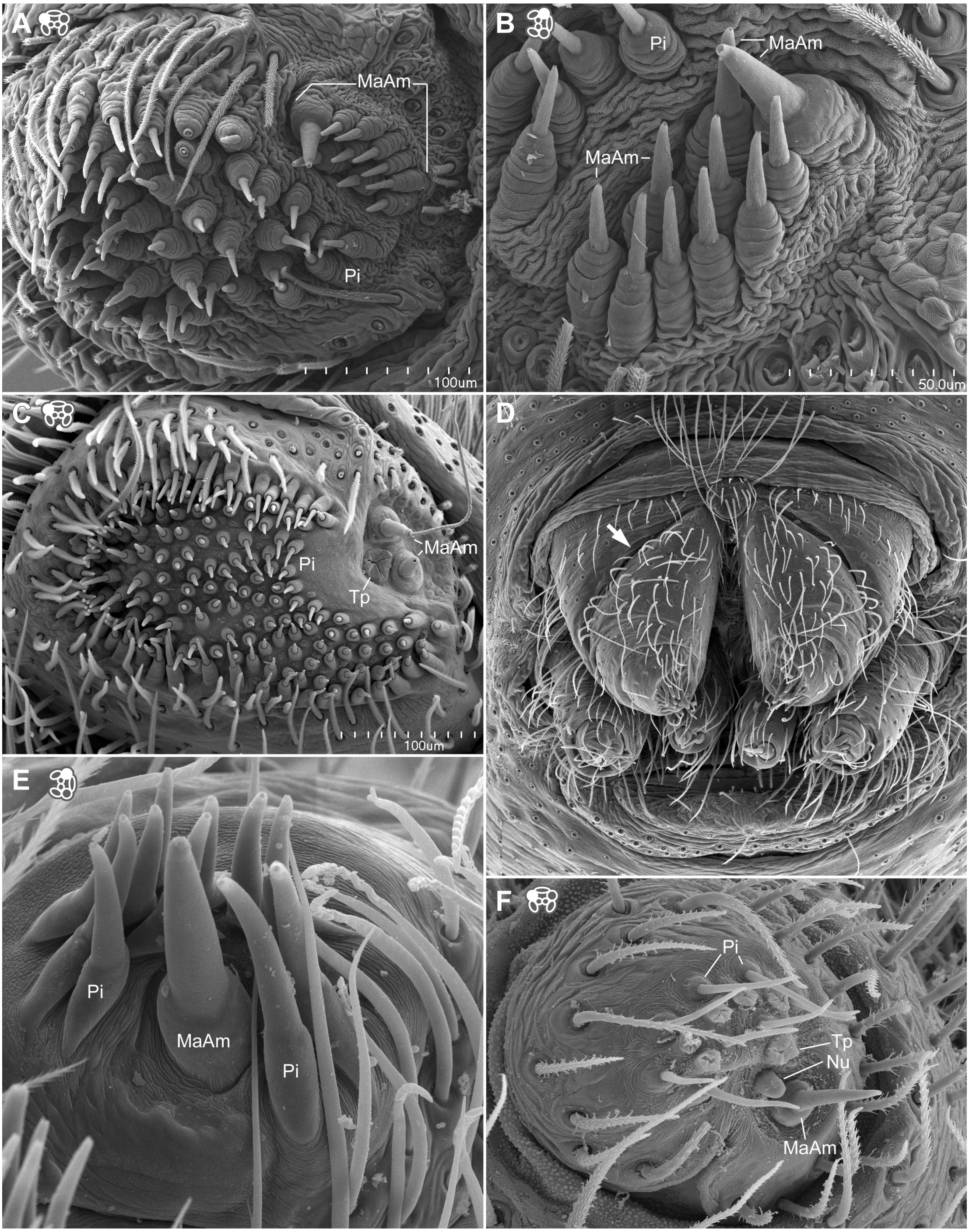

A
MaAm
Pi
100um
B
Pi
MaAm
MaAm
50.0um
C
Pi
MaAm
Tp
100um
D
E
Pi
MaAm
Pi
F
Pi
Tp
Nu
MaAm

Fig. 116. Spinnerets and right ALS spinning field. **A.** *Hypochilus pococki* (Hypochilidae) female ALS. **B.** Same, detail of MaAm field. **C.** *Thaida peculiaris* (Austrochilidae) female ALS. **D.** *Ariadna boesenbergi* (Segestriidae) male spinnerets, arrow to diagonal membranous area on ALS. **E.** *Ariadna boesenbergi* (Segestriidae) female ALS. **F.** *Huttonia* sp. (Huttoniidae) male ALS.

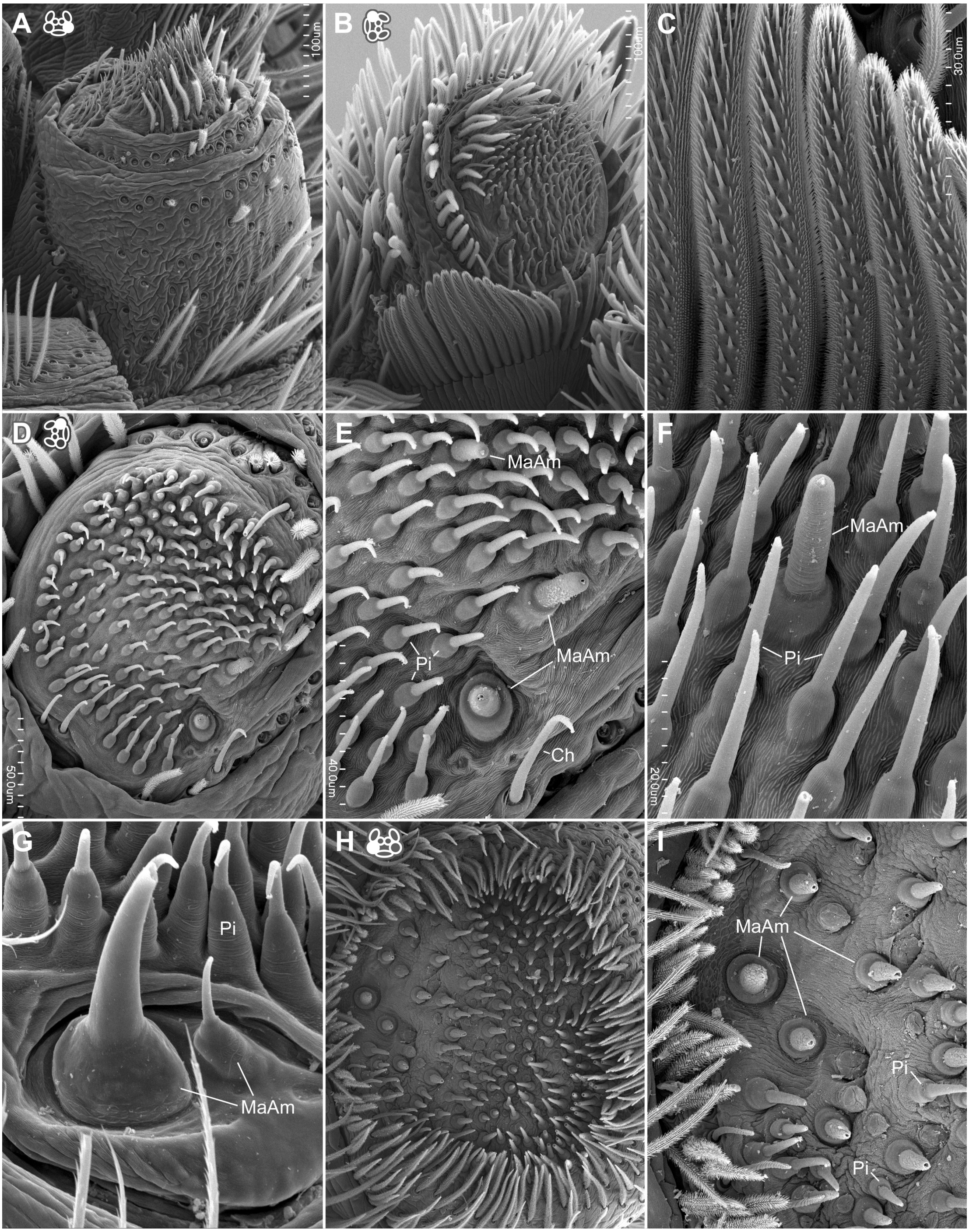

A
100um
B
100um
C
30.0um
D
50.0um
E
MaAm
Pi
MaAm
Ch
40.0um
F
MaAm
Pi
20.0um
G
Pi
MaAm
H
I
MaAm
Pi
Pi

Fig. 117. Structures of ALS, female. **A.** *Filistata insidiatrix* (Filistatidae) right ALS, depilated. **B.** Same, left ALS showing row of thick setae. **C.** Same, detail of modified setae. **D.** Right ALS. **E.** Same, detail of maAm field. **F.** Same, detail of MaAm on Pi field. **G.** *Stedocys leopoldi* (Scytodidae) left MaAm field. **H.** *Eresus* cf. *kollari* (Eresidae) left ALS. **I.** Same, detail of MaAm field.

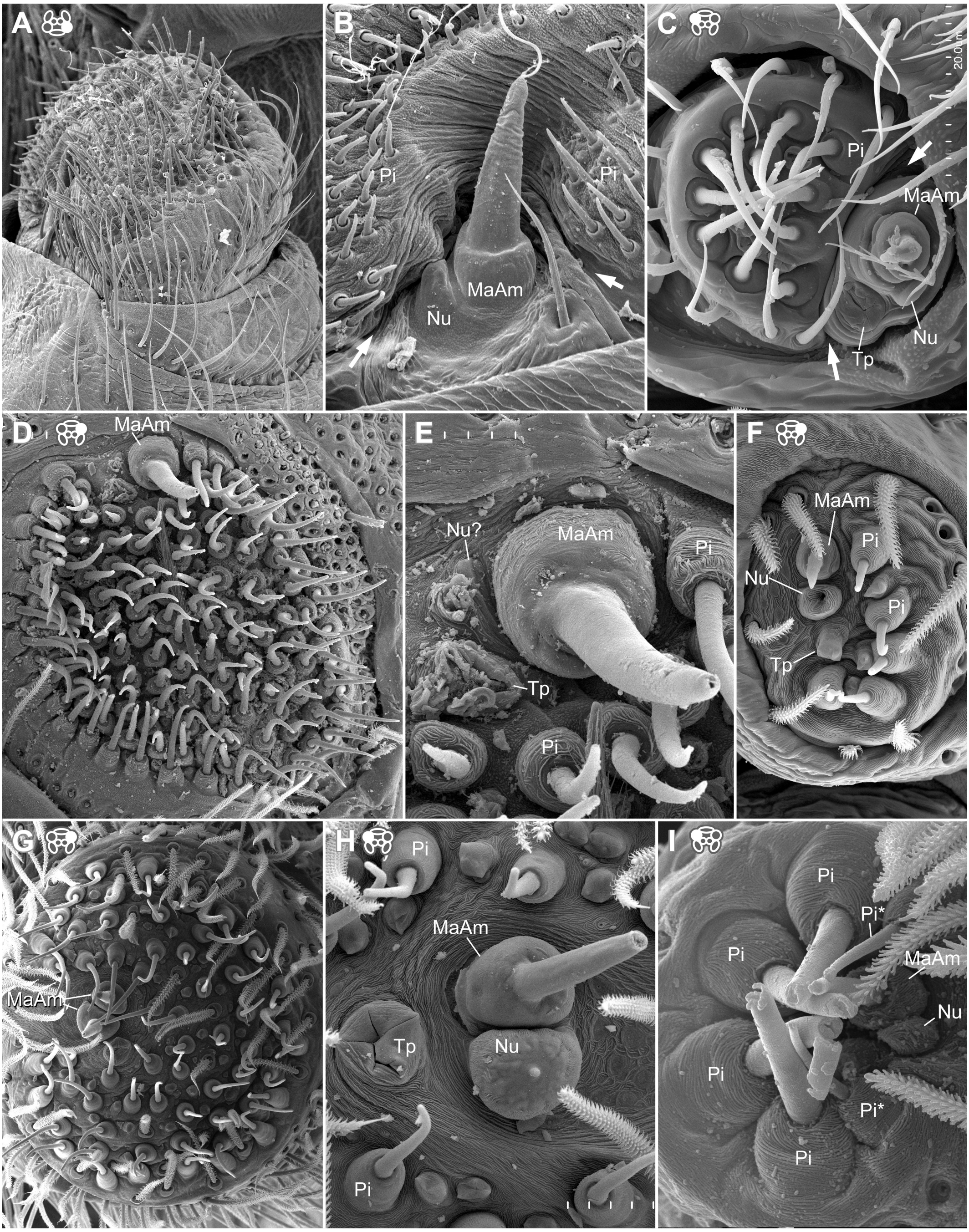

A
B
Pi
Pi
MaAm
Nu
C
Pi
MaAm
Nu
Tp
D
MaAm
E
Nu?
MaAm
Pi
Tp
Pi
F
MaAm
Pi
Nu
Pi
Tp
G
MaAm
H
Pi
MaAm
Tp
Nu
Pi
I
Pi
Pi*
Pi
MaAm
Nu
Pi
Pi*
Pi

Fig. 118. Structures of ALS. **A.** *Araneus* sp. (Araneidae) female right ALS. **B.** Same, MaAm field, arrows to deep furrow between MaAm and Pi fields. **C.** *Crassanapis chilensis* (Anapidae) female right ALS, arrows to deep furrow between MaAm and Pi fields. **D.** *Desis formidabilis* (Desidae) female left ALS. **E.** Same, detail of MaAm field. **F.** *Toxopsiella minuta* (Cycloctenidae) male left ALS. **G.** *Uliodon* cf. *frenatus* (Zoropsidae) female left ALS. **H.** *Uliodon* cf. *frenatus* (Zoropsidae) male right MaAm field. **I.** *Ciniflella* BRA (Tengellidae) male right ALS.

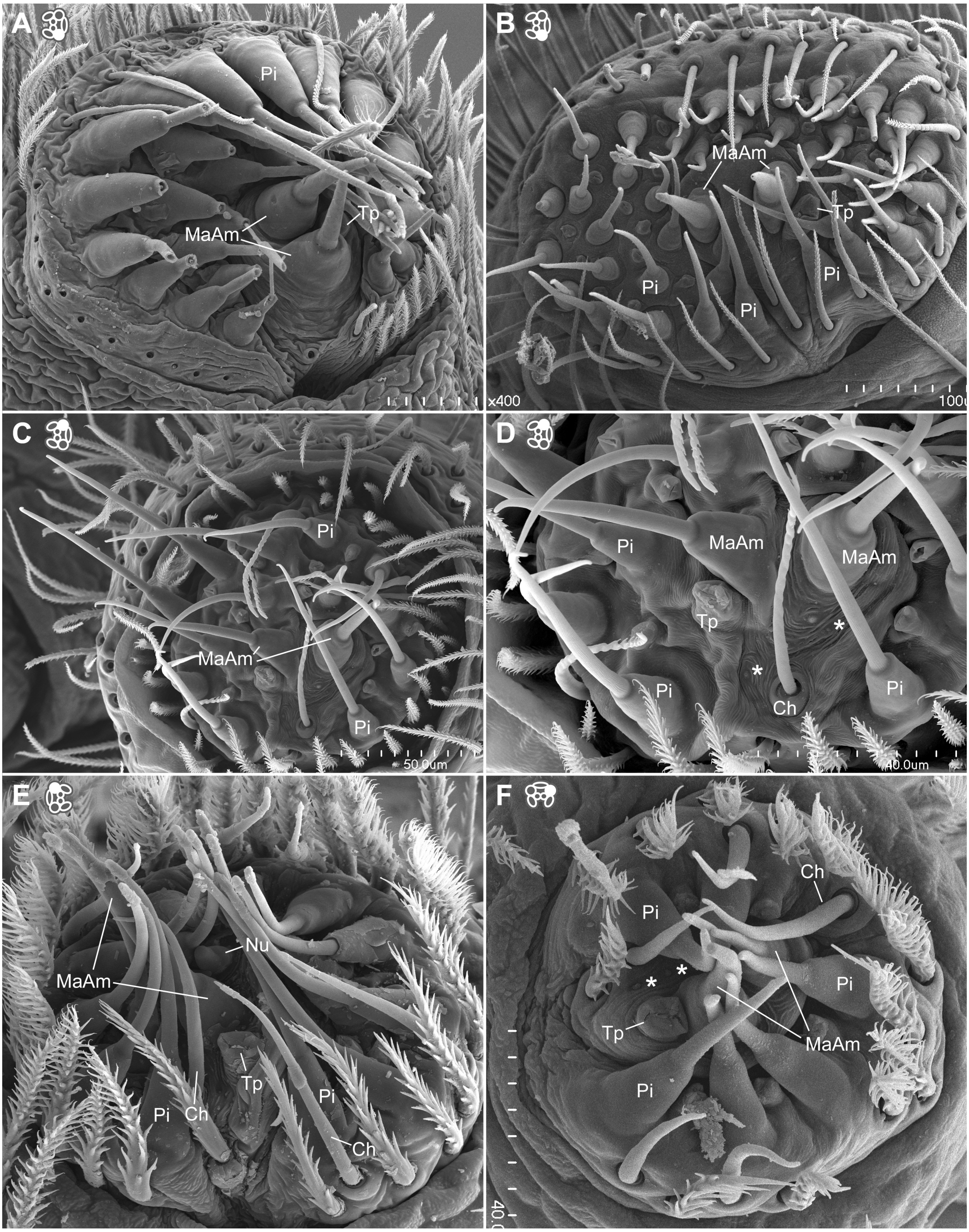

A
Pi
Tp
MaAm
B
MaAm
Tp
Pi
Pi
Pi
x400
C
Pi
MaAm
Pi
50.0um
D
Pi
MaAm
MaAm
Tp
*
*
Pi
Ch
Pi
40.0um
E
Nu
MaAm
Tp
Pi
Pi
Ch
Ch
F
Ch
Pi
*
*
Pi
Tp
MaAm
Pi

Fig. 119. ALS spinning field of Homalonychidae and Zodariidae. **A.** *Homalonychus theologus* (Homalonychidae) female left ALS. **B.** *Storenomorpha arboccoae* (Zodariidae) female left ALS. **C.** *Cyrioctea aschaensis* (Zodariidae) female right ALS. **D.** Same, detail of MaAm field invaginated among piriform spigots, asterisks on MaAm field sensilla. **E.** *Cryptothele alluaudi* (Zodariidae) female, left ALS. **F.** Same, immature, left ALS, asterisks on MaAm field sensilla.

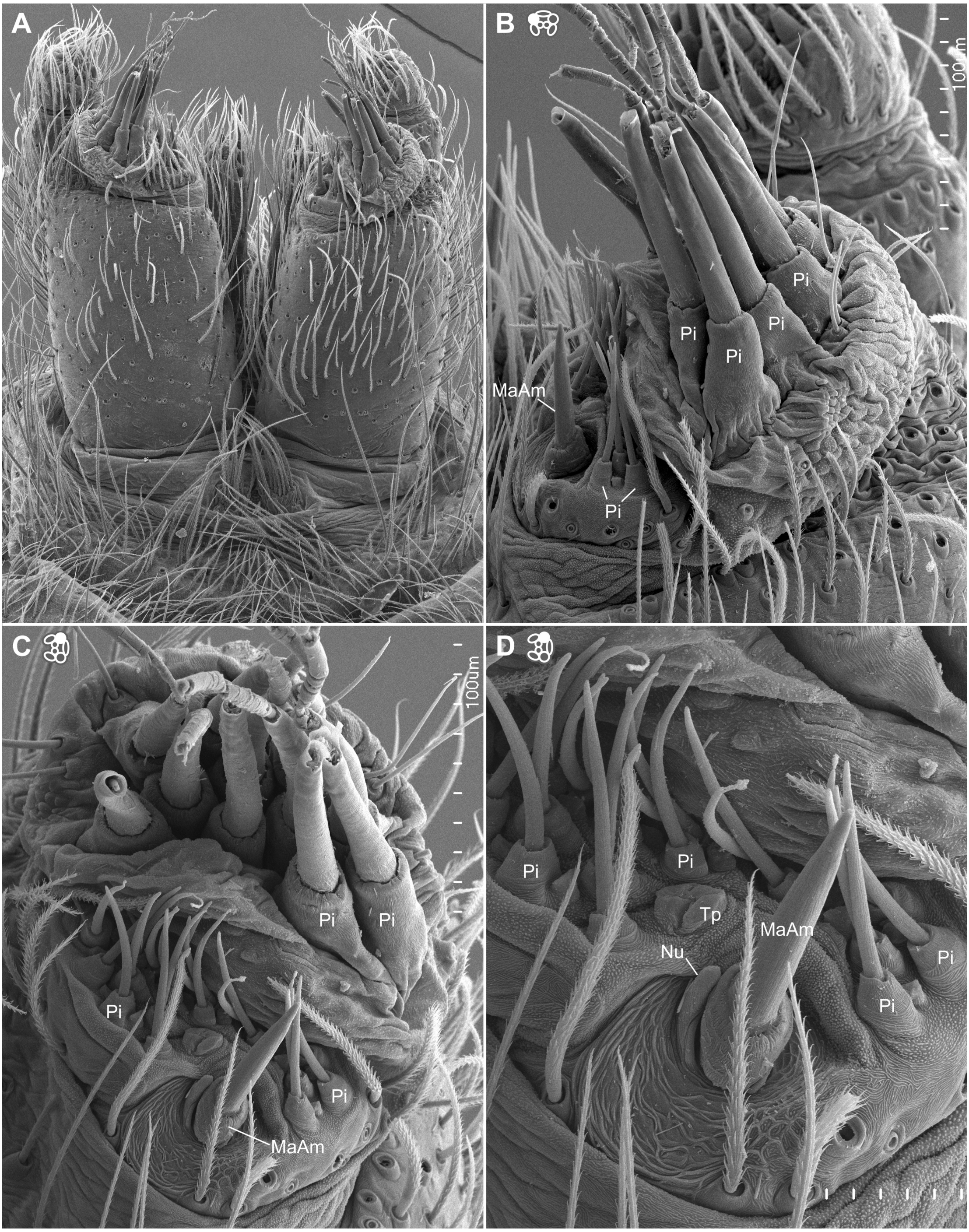

A
B
Pi
Pi
Pi
Pi
MaAm
Pi
100um
C
Pi
Pi
Pi
Pi
MaAm
100um
D
Pi
Pi
Tp
MaAm
Nu
Pi
Pi

Fig. 120. *Clubiona pallidula* (Clubionidae) male ALS. **A.** Ventral view. **B.** Same, right ALS spinning field. **C.** Same, mesal view. **D.** Same, detail of MaAm field with smaller piriform spigots.

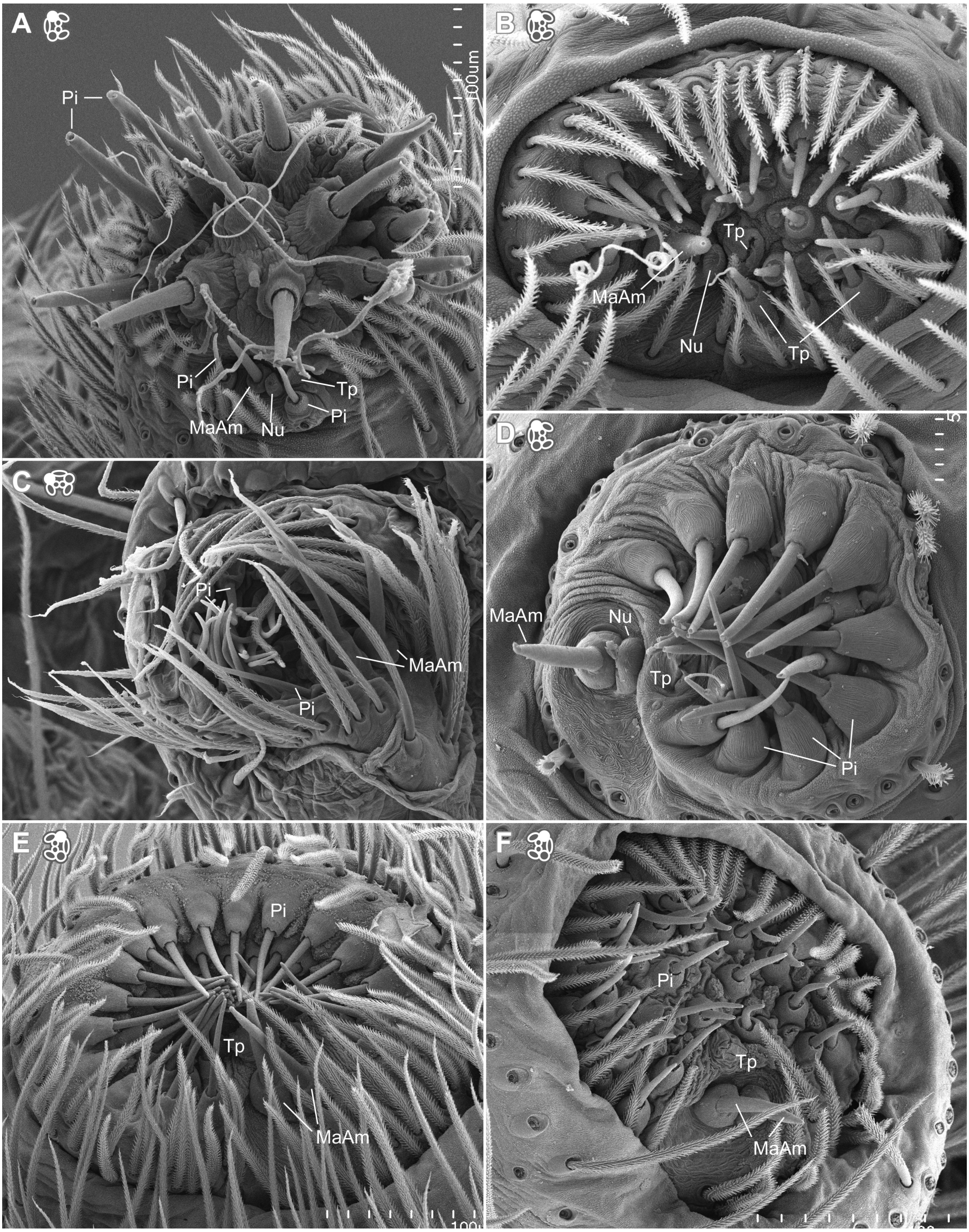

A
100um
Pi
Pi
Tp
MaAm
Nu
Pi
B
Tp
MaAm
Nu
Tp
C
Pi
MaAm
Pi
D
5
MaAm
Nu
Tp
Pi
E
Pi
Tp
MaAm
F
Pi
Tp
MaAm

Fig. 121. ALS spinning field. **A.** *Agroeca brunnea* ("Liocranidae") male, left. **B.** *Donuea* sp. ("Liocranidae") male, left. **C.** *Systaria* sp. (Miturgidae) female, right. **D.** Same, male, left. **E.** *Teminius insularis* (Miturgidae) female, right. **F.** Same, male, right.

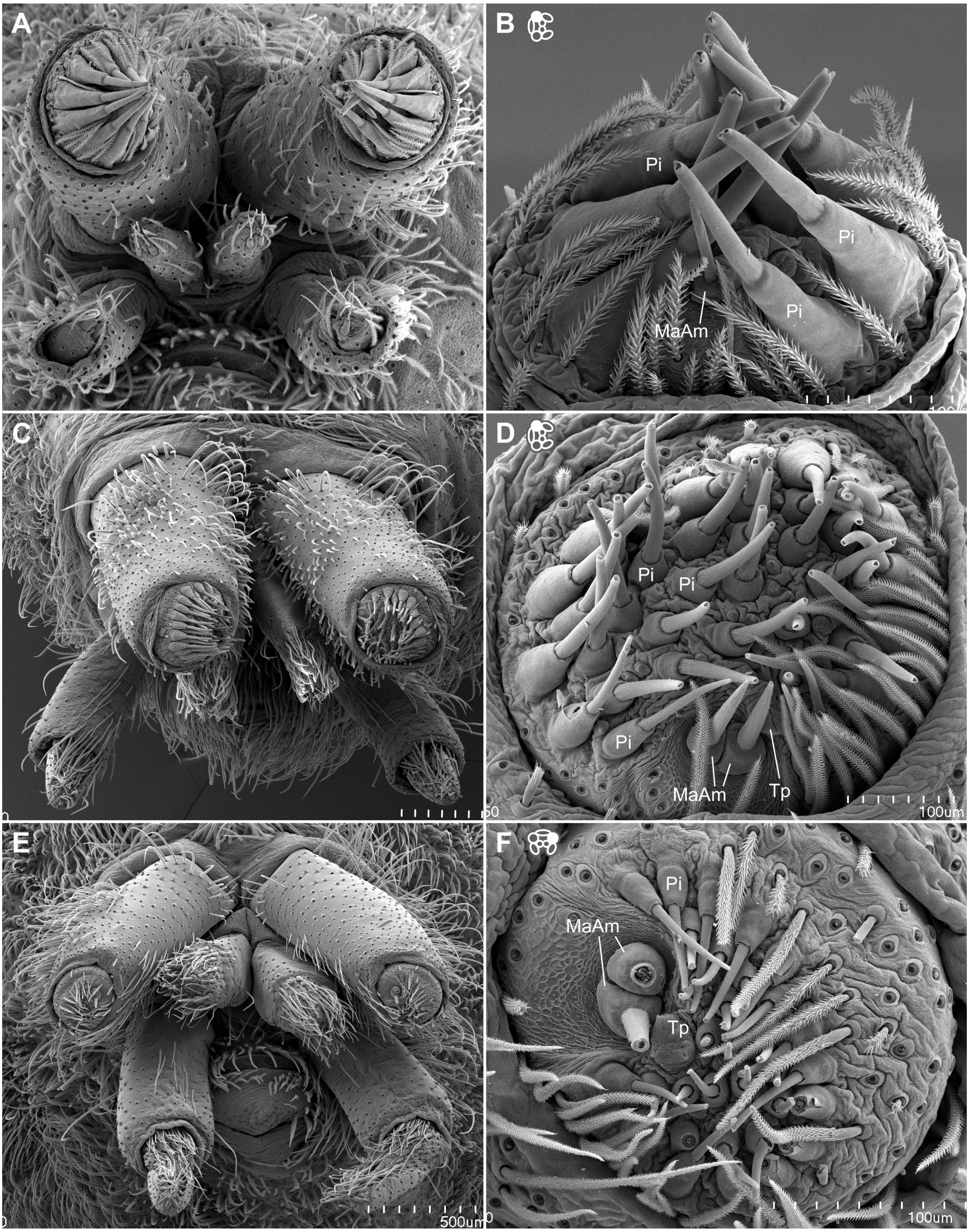

A
B
Pi
Pi
Pi
MaAm
C
D
Pi
Pi
Pi
MaAm
Tp
100um
E
500um
F
Pi
MaAm
Tp
100um

Fig. 122. Spinnerets and left ALS of Miturgidae. **A.** Miturgidae QLD, male spinnerets. **B.** Same, ALS. **C.** *Miturga gilva*, male spinnerets. **D.** Same, ALS. **E.** Same, female spinnerets. **F.** Same, ALS.

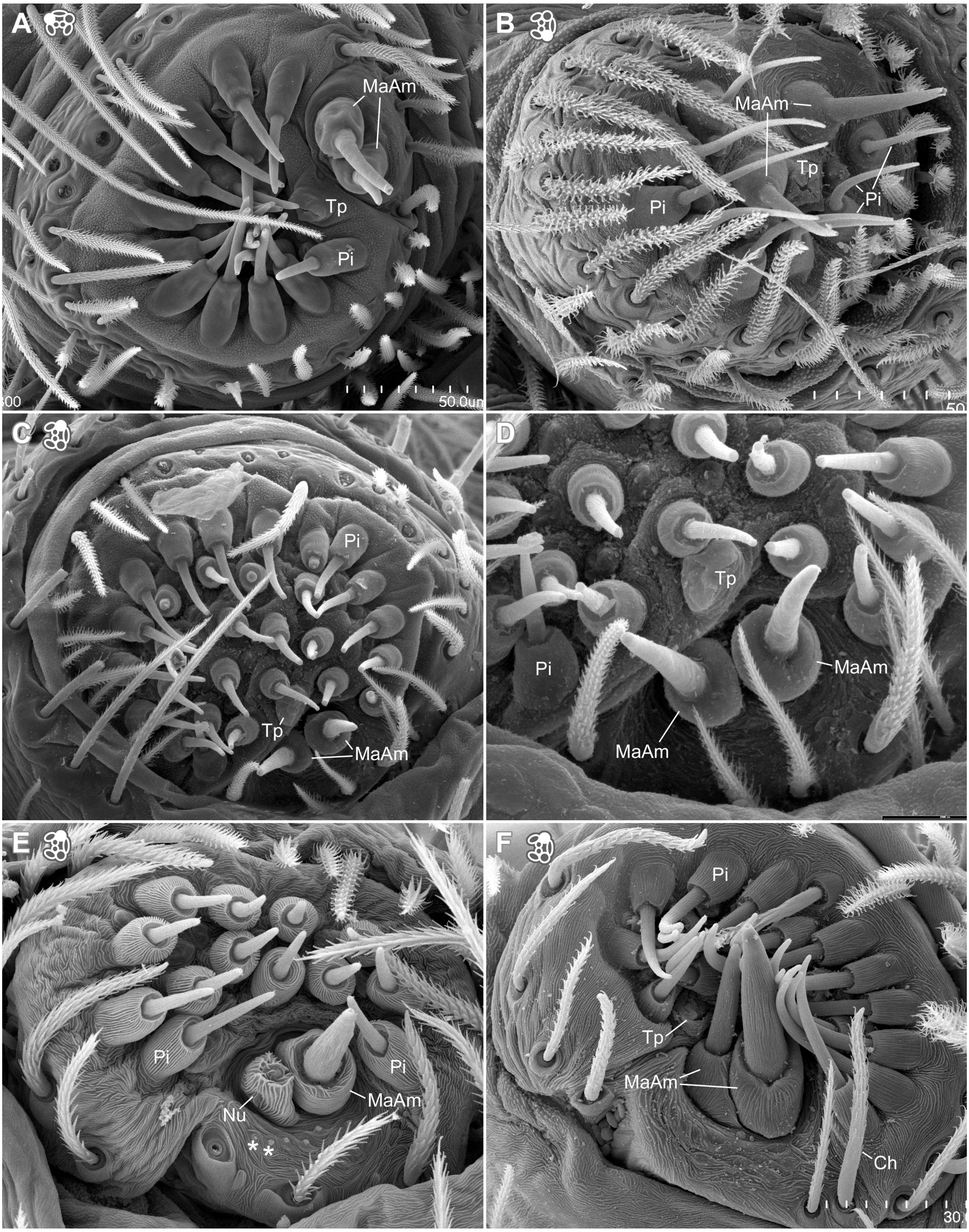

A
MaAm
Tp
Pi
50.0um
B
MaAm
Tp
Pi
Pi
C
Pi
Tp
MaAm
D
Tp
Pi
MaAm
MaAm
E
Pi
Pi
Nu
MaAm
* *
F
Pi
Tp
MaAm
Ch

Fig. 123. ALS spinning field, female. **A.** *Brachyphaea* cf. *simoni* (Corinnidae) right ALS. **B.** *Oedignatha* cf. *jocquei* (Liocranidae) left. **C.** *Falconina gracilis* (Corinnidae), right. **D.** Same, detail of MaAm field. **E.** *Malenella nana* (Anyphaenidae) right; asterisks on MaAm field sensilla. **F.** *Hispo* sp. (Salticidae) right.

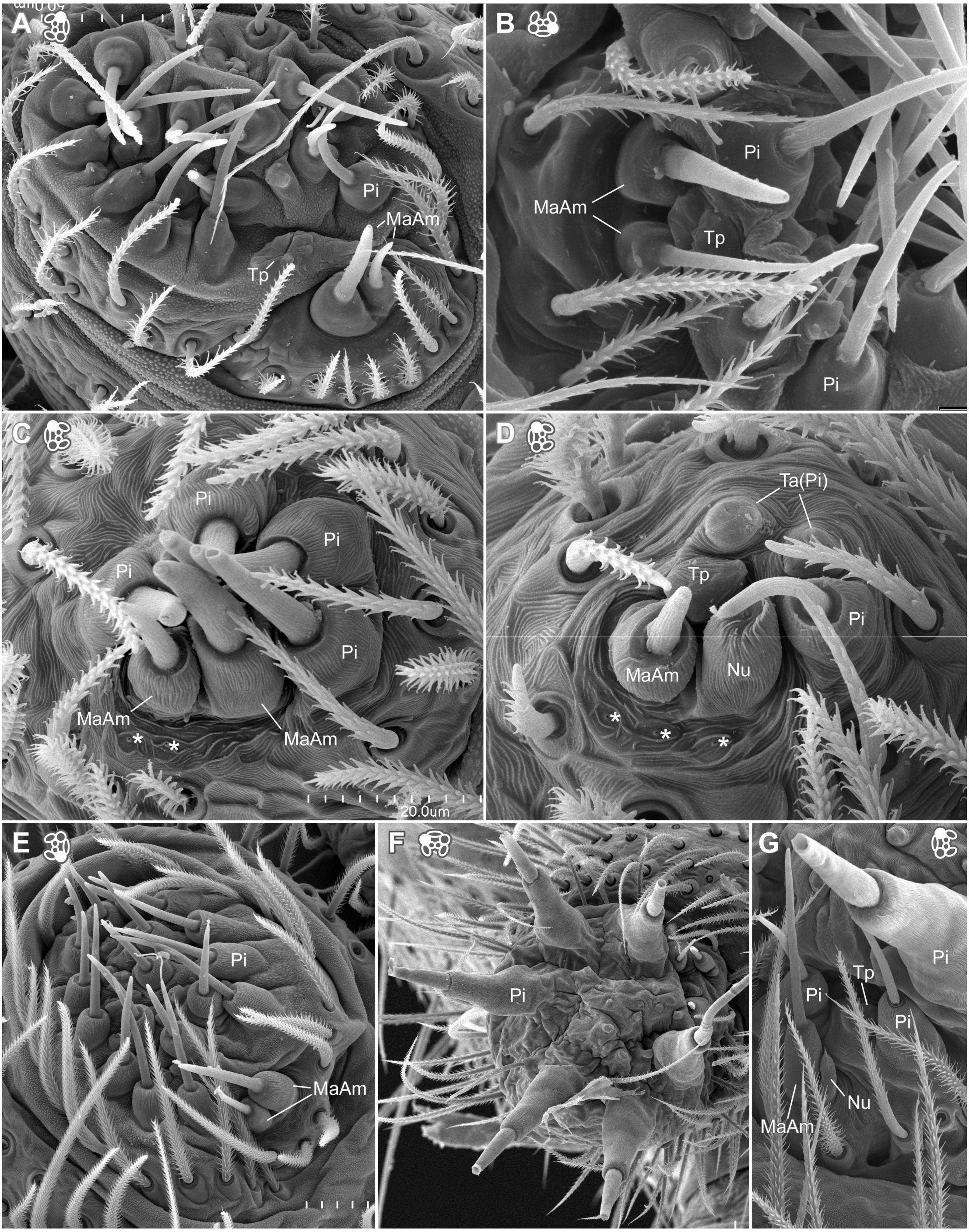

A
Pi
MaAm
Tp
B
Pi
MaAm
Tp
Pi
C
Pi
Pi
Pi
Pi
MaAm
MaAm
*
*
20.0um
D
Ta(Pi)
Tp
Pi
MaAm
Nu
*
*
*
E
Pi
MaAm
F
Pi
G
Pi
Tp
Pi
Pi
Nu
MaAm

Fig. 124. ALS spinning field of "Liocranidae." **A.** *Sesieutes* sp. female, right ALS. **B.** *Teutamus* sp. female, right MaAm field. **C.** *Apostenus californicus* female, left; asterisks on MaAm field sensilla. **D.** Same, male, left. **E.** *Toxoniella* sp. female, left. **F.** Same, male, right. **G.** Same, detail of left MaAm field.

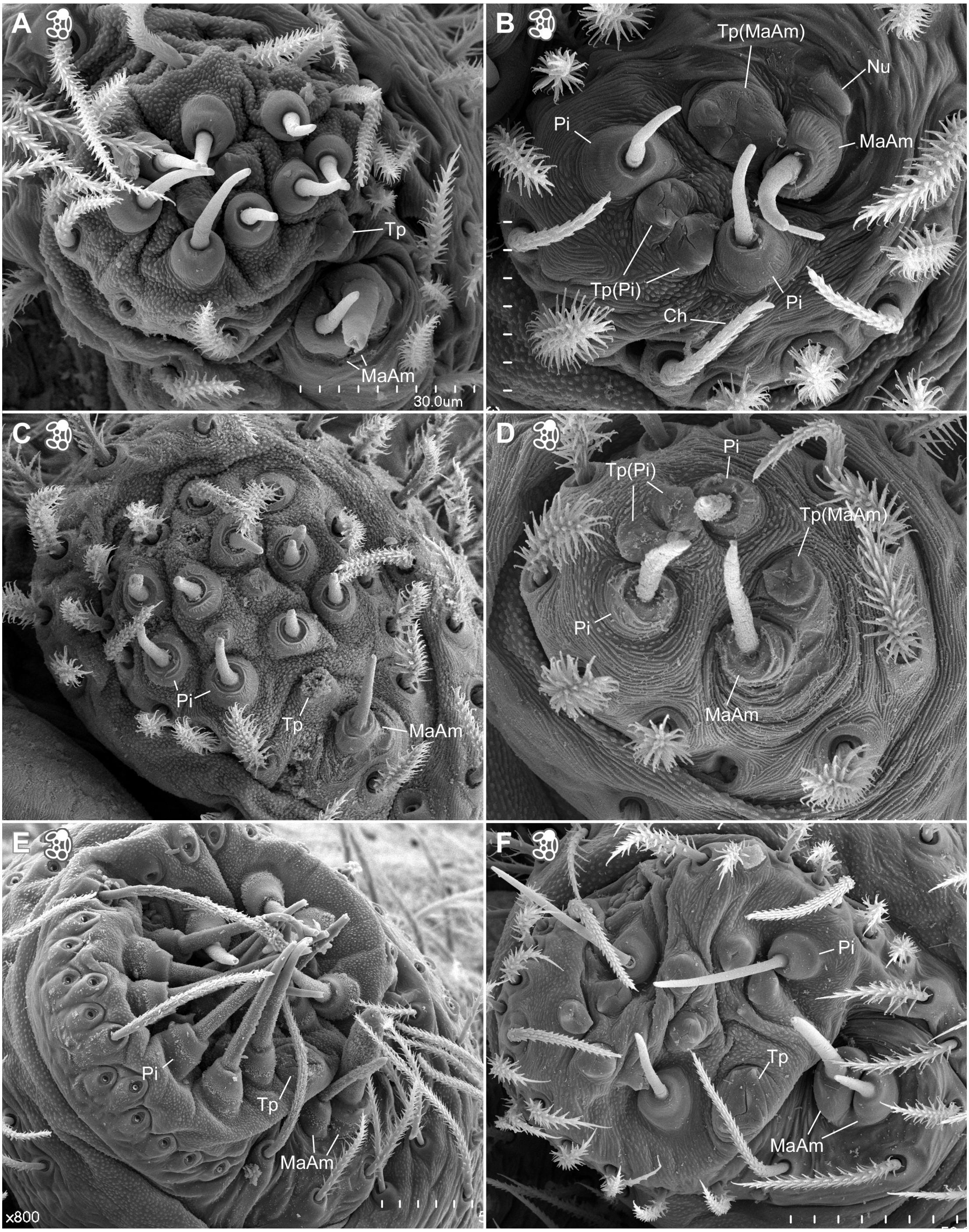

A
Tp
MaAm
30.0um
B
Tp(MaAm)
Nu
Pi
MaAm
Tp(Pi)
Pi
Ch
C
Pi
Tp
MaAm
D
Pi
Tp(Pi)
Tp(MaAm)
Pi
MaAm
E
Pi
Tp
MaAm
x800
F
Pi
Tp
MaAm

Fig. 125. ALS spinning fields of Phrurolithidae. **A.** *Phrurolithus festivus* female, right ALS. **B.** Same, male, left. **C.** *Phrurotimpus alarius* female, right. **D.** Same, male, right. **E.** *Otacilia* sp. female, right. **F.** Same, male, right.

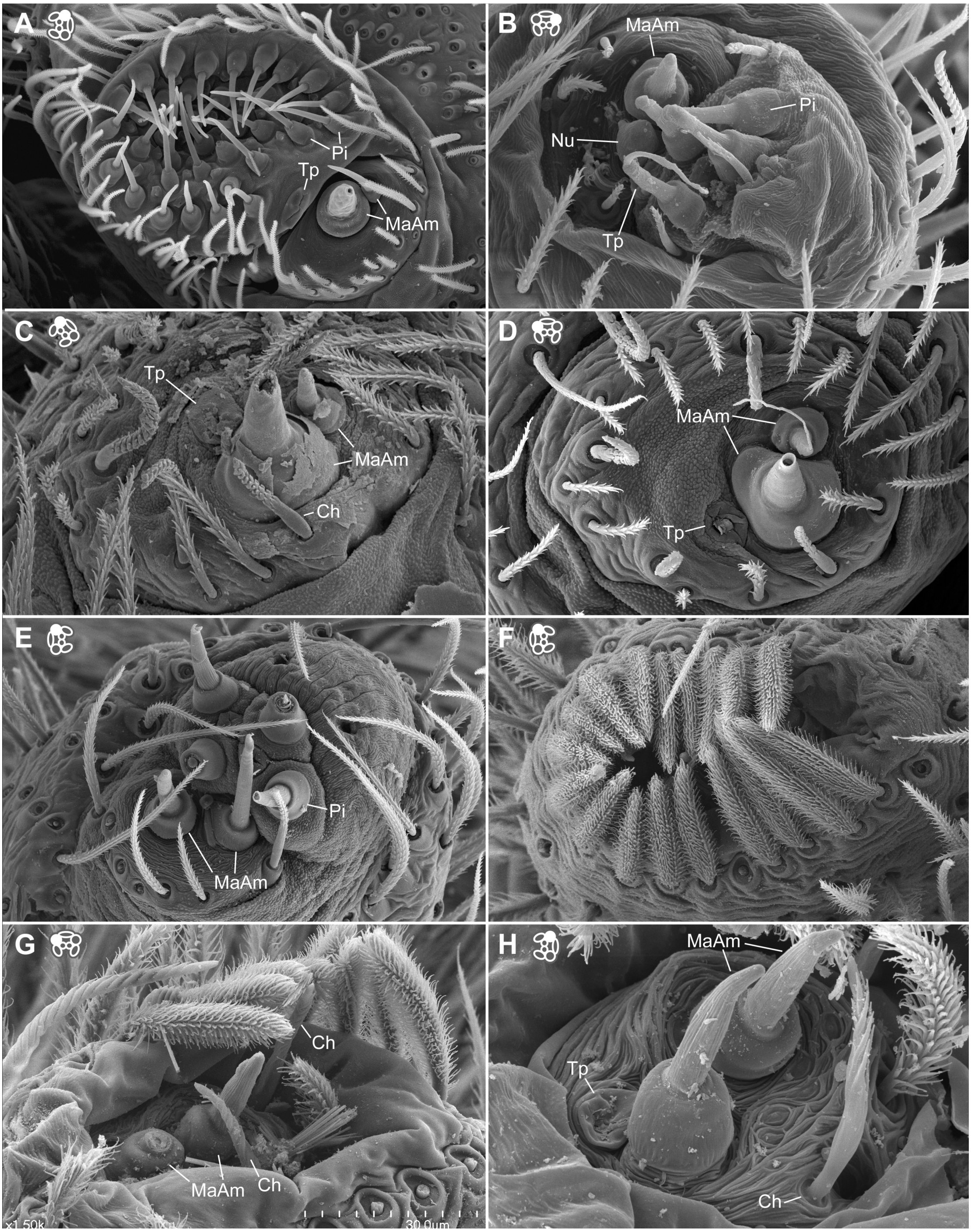

A
Pi
Tp
MaAm
B
MaAm
Pi
Nu
Tp
C
Tp
MaAm
Ch
D
MaAm
Tp
E
Pi
MaAm
F
G
Ch
MaAm
Ch
x1.50k
30.0um
H
MaAm
Tp
Ch

Fig. 126. ALS spinning fields. **A.** *Austrachelas pondoensis* (Gallieniellidae) female, right ALS. **B.** *Platyoides walteri* (Trochanteriidae) male, left. **C.** *Galianoella leucostigma* (Gallieniellidae) female, right. **D.** Same, male, right. **E.** *Cithaeron delimbatus* (Cithaeronidae) female, left. **F.** *Ammoxenus amphalodes* (Ammoxenidae) female, left. **G.** Same, right. **H.** Same, male, right.

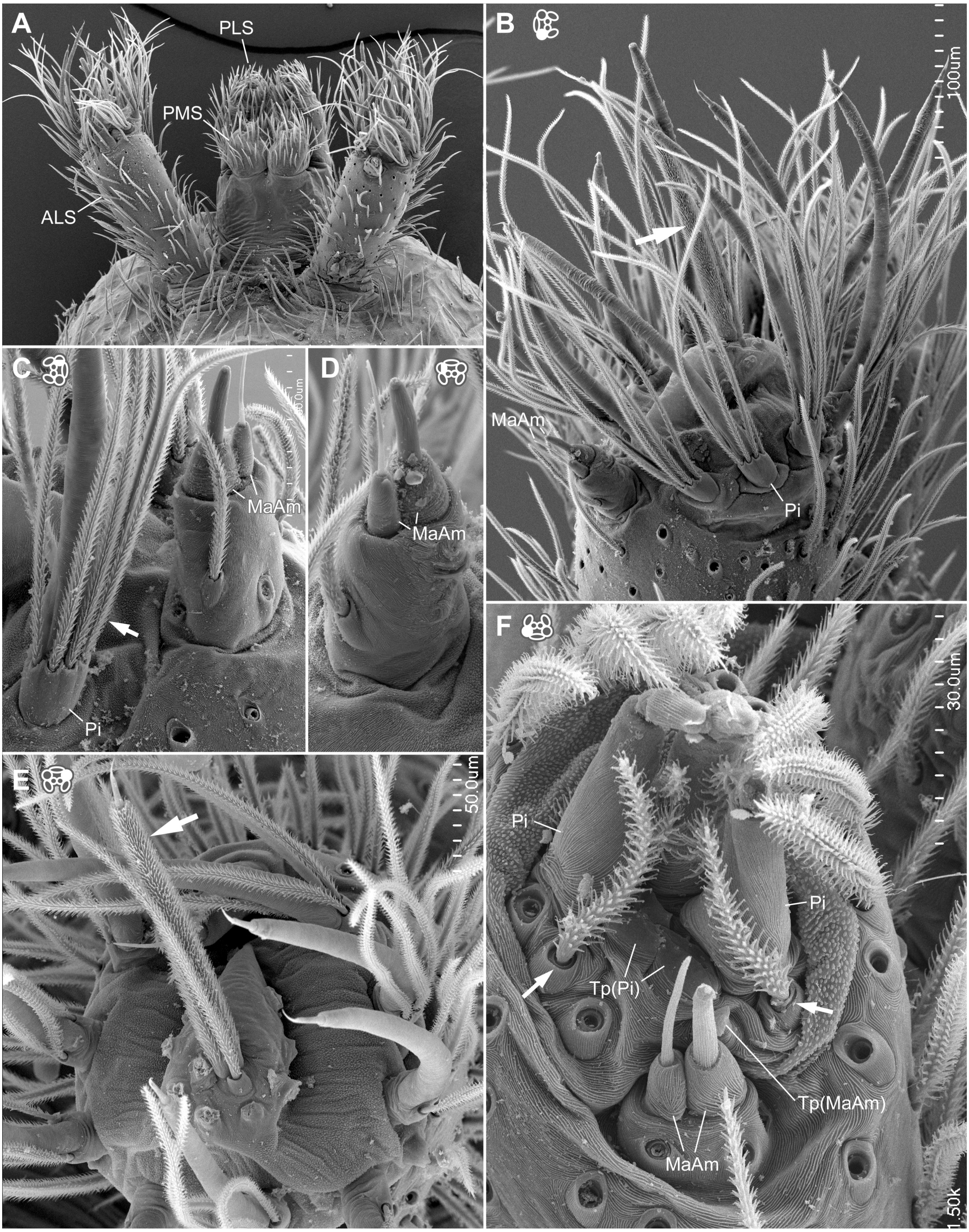

A
PLS
PMS
ALS
B
100um
MaAm
Pi
C
50.0um
MaAm
Pi
D
MaAm
E
50.0um
F
30.0um
Pi
Pi
Tp(Pi)
Tp(MaAm)
MaAm
1.50k

Fig. 127. Spinnerets of Prodidomidae. **A.** *Lygromma* sp., female spinnerets. **B.** Same, female right ALS, arrow to Pi spigot with plumose base. **C.** Same, right MaAm field and Pi base, arrow to setae encircling Pi base. **D.** Same, right MaAm field. **E.** Same, male left ALS field, arrow to Pi spigot with plumose base. **F.** Cf. *Moreno* ARG, female left ALS, arrows to setae flanking spigot base.

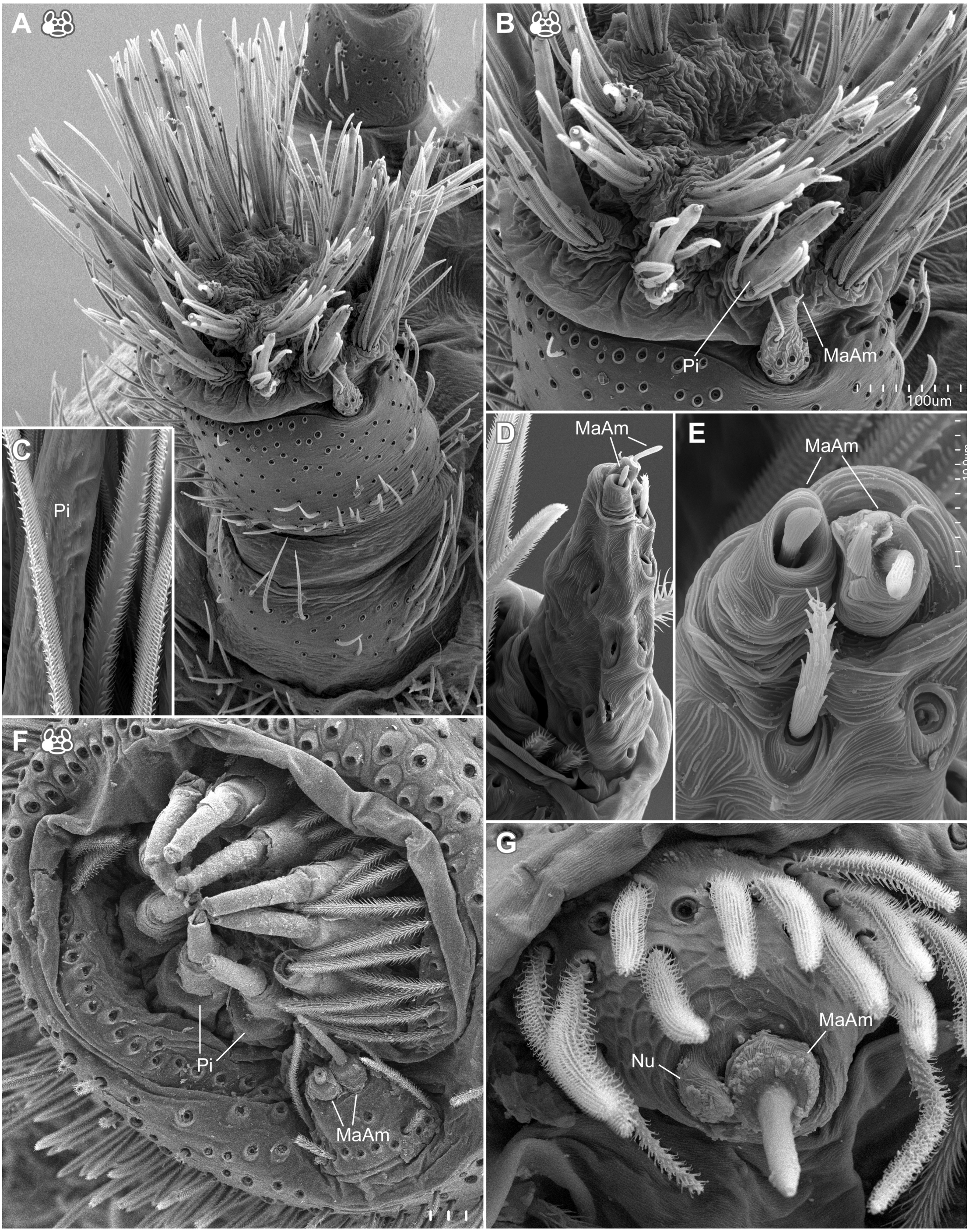

A
B
Pi
MaAm
100um
C
Pi
D
MaAm
E
MaAm
F
Pi
MaAm
G
MaAm
Nu

Fig. 128. Structures of ALS of Prodidomidae. **A.** *Neozimiris pubescens* female left ALS. **B.** Same, detail of spinning field. **C.** *Prodidomus redikorzevi* female right ALS, detail of piriform spigot and flanking setae. **D.** Same, male right MaAm field. **E.** Same, detail of MaAm spigots. **F.** *Anagraphis pallens* female left ALS. **G.** Same, male left MaAm field.

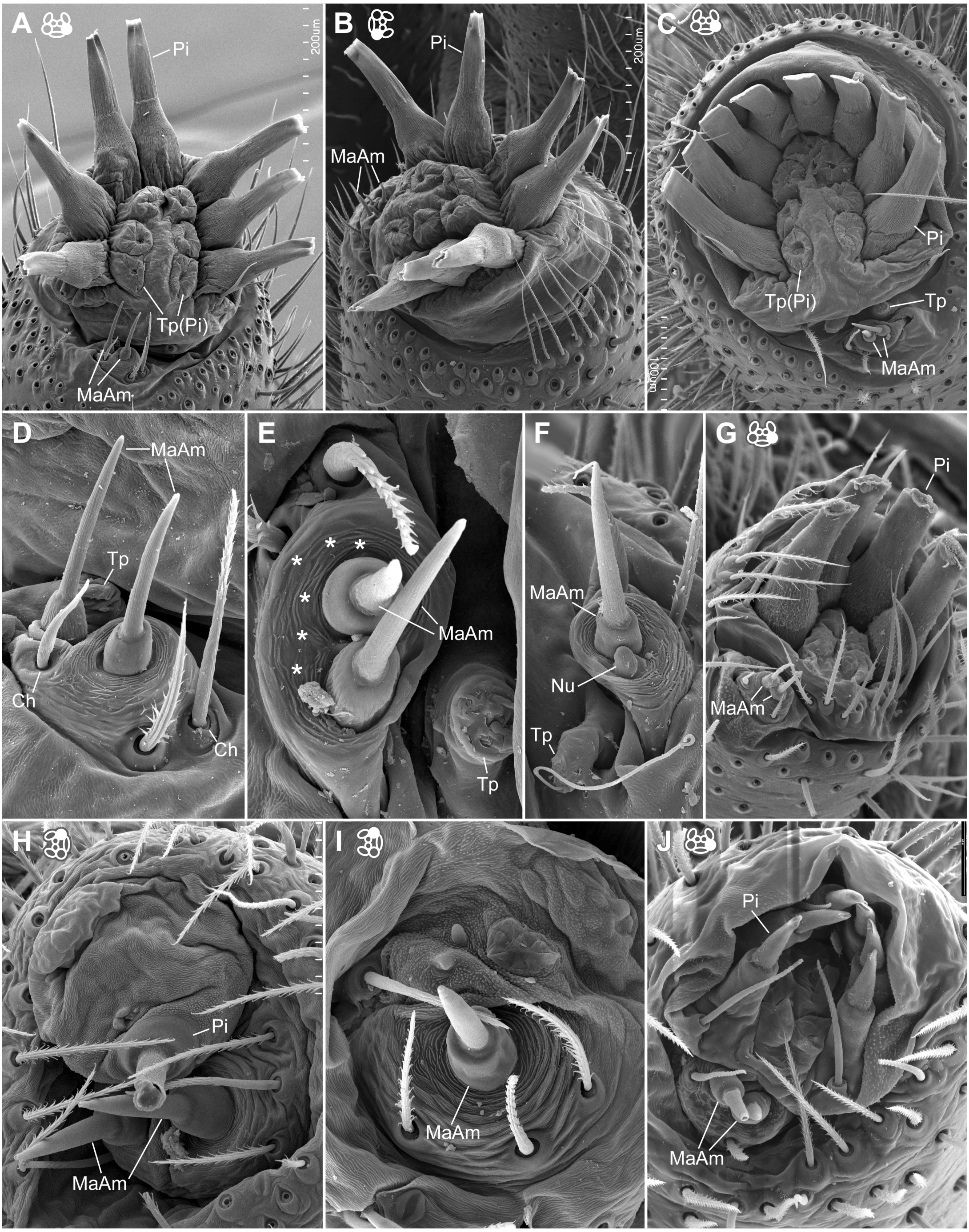

A
Pi
200um
Tp(Pi)
MaAm
B
Pi
200um
MaAm
C
Pi
Tp(Pi)
Tp
MaAm
100um
D
MaAm
Tp
Ch
Ch
E
MaAm
Tp
F
MaAm
Nu
Tp
G
Pi
MaAm
H
Pi
MaAm
I
MaAm
J
Pi
MaAm

Fig. 129. Structures of ALS of Gnaphosidae. **A.** *Gnaphosa taurica* female right ALS with expanded Pi field, anterior. **B.** Same, ectal. **C.** Same, left ALS with collapsed Pi field. **D.** Same, right MaAm field. **E.** Same, left MaAm field; asterisks at sensilla. **F.** Same, male right MaAm field. **G.** *Camillina calel* female right ALS. **H.** *Micaria fulgens* female right ALS. **I.** Same, male right ALS. **J.** *Vectius niger* female right ALS.

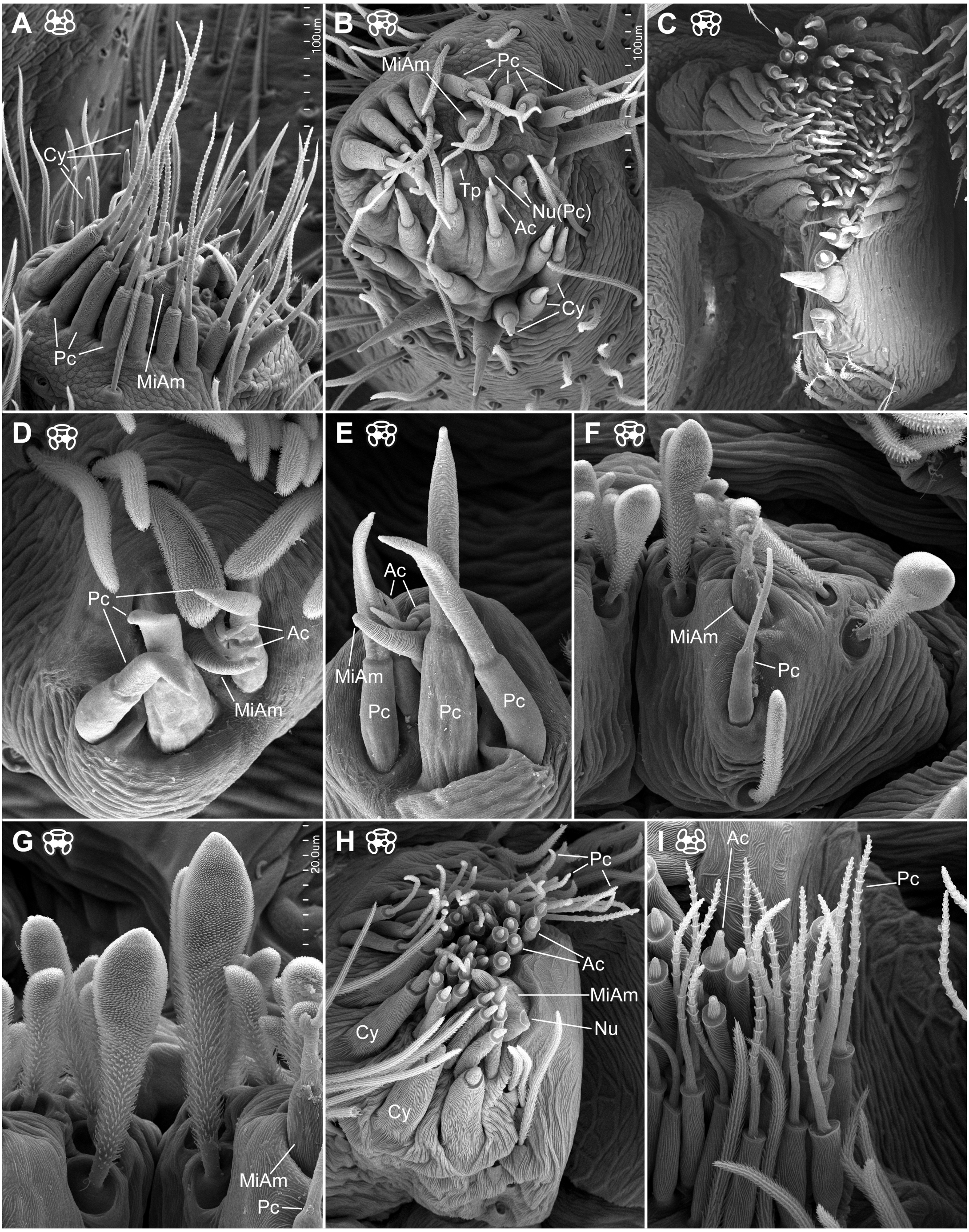

A
100um
Cy
Pc
MiAm
B
100um
MiAm
Pc
Tp
Nu(Pc)
Ac
Cy
C
D
Pc
Ac
MiAm
E
Ac
MiAm
Pc
Pc
Pc
F
MiAm
Pc
G
20.0um
MiAm
Pc
H
Pc
Ac
MiAm
Nu
Cy
Cy
I
Ac
Pc

Fig. 130. PMS spinning field and setae. **A.** *Thaida peculiaris* (Austrochilidae) female, left PMS, anterior. **B.** Same, right. **C.** *Araneus diadematus* (Araneidae) male, right. **D.** *Filistata insidiatrix* (Filistatidae) female, left. **E.** Same, right, posterior. **F.** *Pritha nana* (Filistatidae) female, left. **G.** Same, modified setae on PMS, anterior. **H.** *Uloborus glomosus* (Uloboridae) female, right. **I.** Same, left, detail of spigots, anterior.

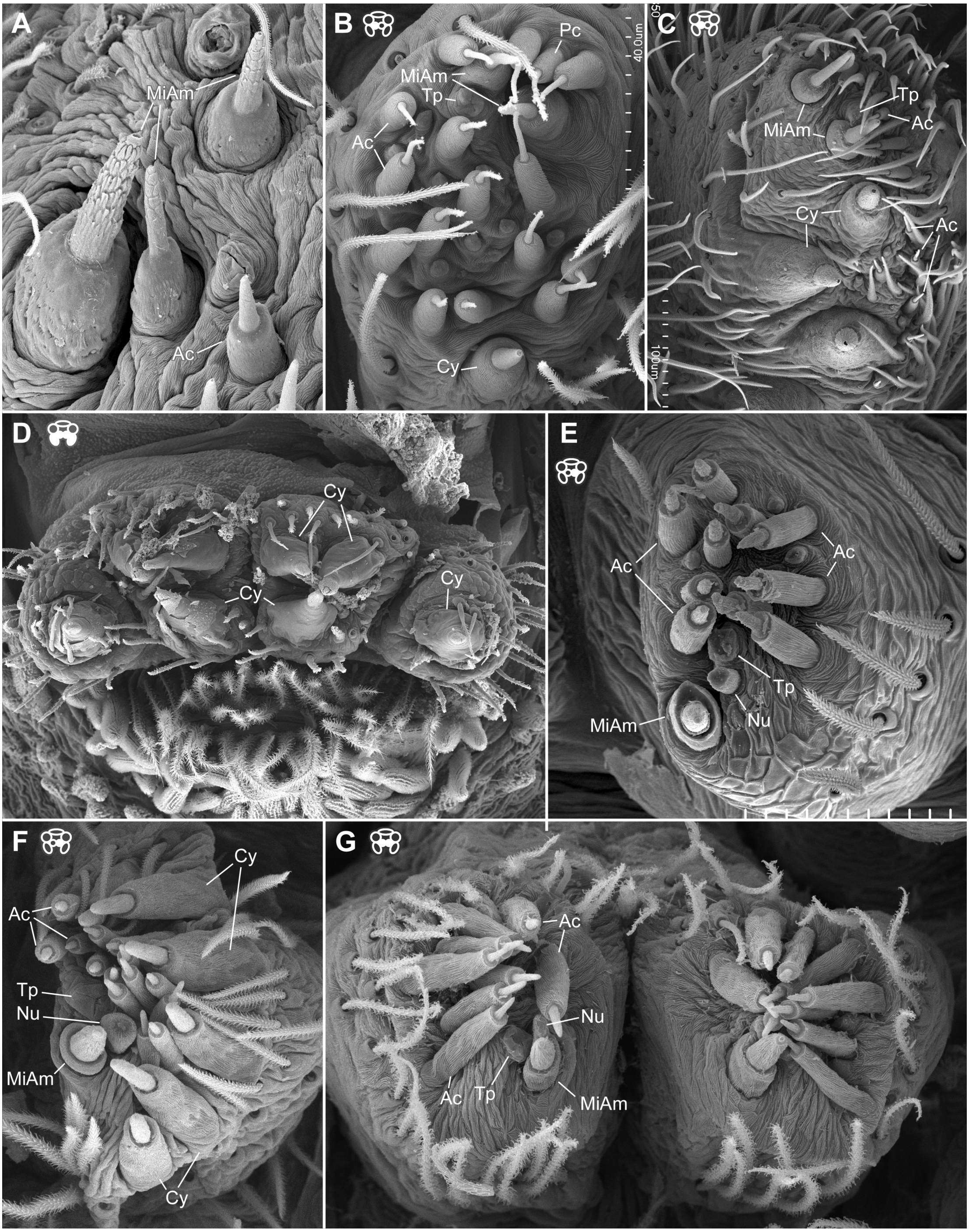

A
MiAm
Ac
B
Pc
MiAm
Tp
Ac
Cy
40.0um
C
Tp
Ac
MiAm
Cy
Ac
100um
D
Cy
Cy
Cy
E
Ac
Ac
Tp
Nu
MiAm
F
Cy
Ac
Tp
Nu
MiAm
Cy
G
Ac
Nu
Ac
Tp
MiAm

Fig. 131. PMS spinning field. **A.** *Eresus* cf. *kollari* (Eresidae) female, left PMS, detail. **B.** *Pimus napa* (Amaurobiidae) female, right. **C.** *Zorocrates gnaphosoides* (Zorocratidae) female, left. **D.** *Cryptothele* sp. Sri Lanka (Zodariidae) female PMS and PLS. **E.** *Oxyopes heterophthalmus* (Oxyopidae) male, left. **F.** *Senoculus* sp. (Senoculidae) female, left. **G.** Same, male, both PMS.

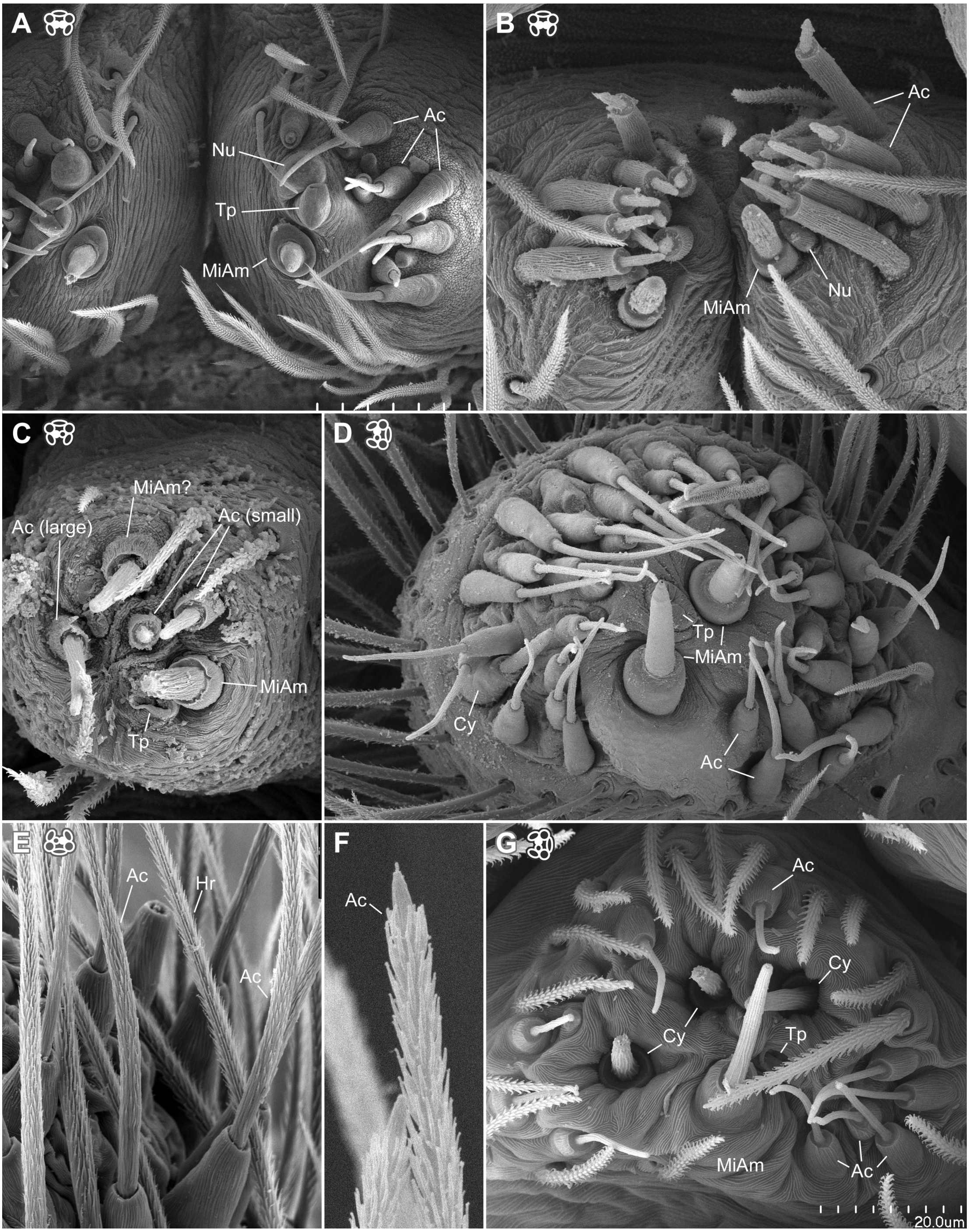

A
Ac
Nu
Tp
MiAm
B
Ac
MiAm
Nu
C
MiAm?
Ac (large)
Ac (small)
MiAm
Tp
D
Tp
MiAm
Cy
Ac
E
Ac
Hr
Ac
F
Ac
G
Ac
Cy
Cy
Tp
MiAm
Ac
20.0um

Fig. 132. PMS spinning field. **A.** *Borboropactus bituberculatus* (Thomisidae) male. **B.** *Geraesta hirta* (Thomisidae) male. **C.** *Lyssomanes viridis* (Salticidae) male, right PMS. **D.** *Eutichurus lizeri* (Eutichuridae) female, right. **E.** *Strotarchus piscatorius* (Eutichuridae) female, right, aciniform spigots, anterior. **F.** Same, detail of shaft of aciniform spigot. **G.** *Hortipes merwei* ("Corinnidae") female, right.

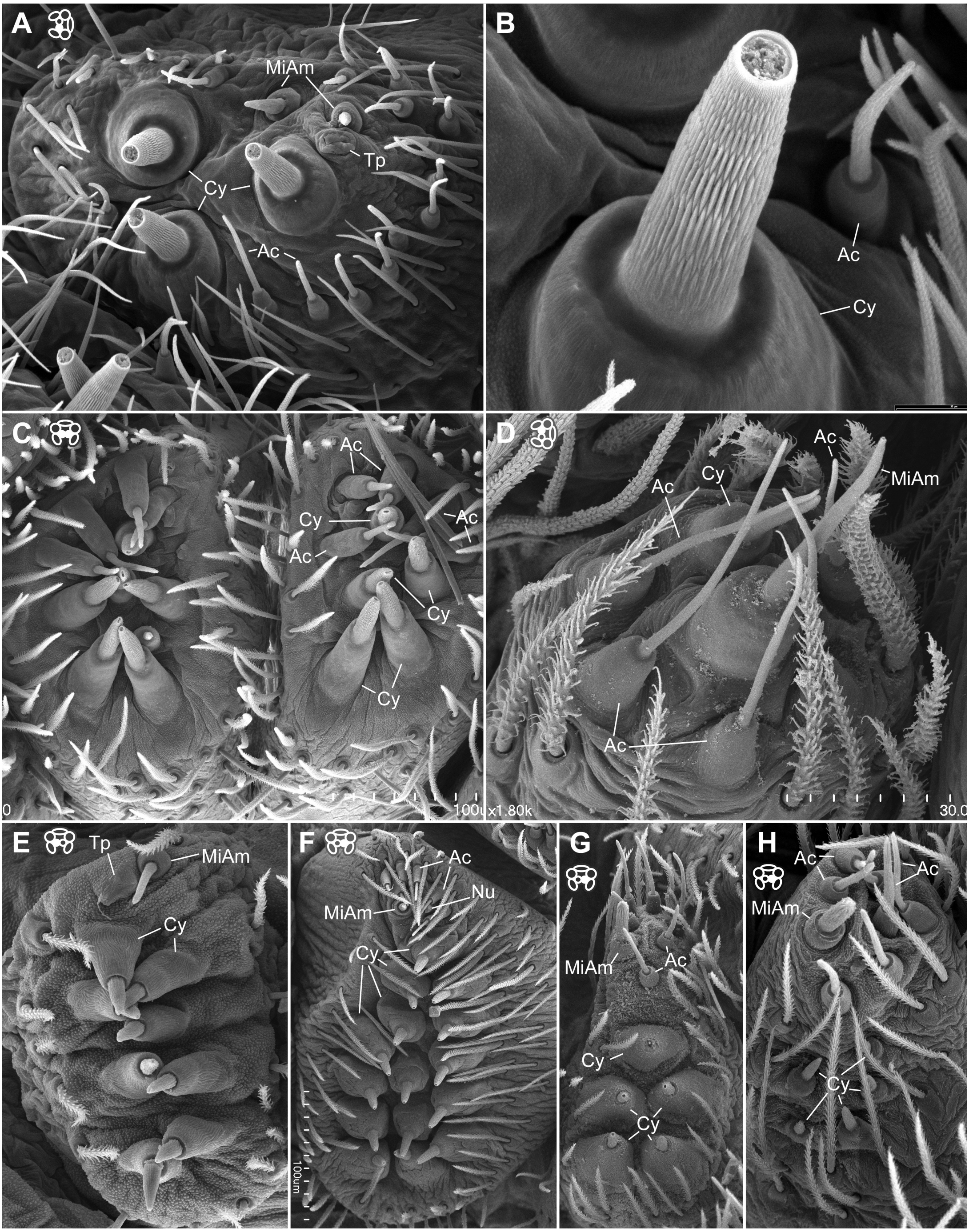

A
MiAm
Tp
Cy
Ac
B
Ac
Cy
C
Ac
Cy
Ac
Ac
Cy
Cy
100u
D
Ac
Cy
Ac
MiAm
Ac
x1.80k
30.0
E
Tp
MiAm
Cy
F
Ac
Nu
MiAm
Cy
100um
G
MiAm
Ac
Cy
Cy
H
Ac
Ac
MiAm
Cy

Fig. 133. PMS spinning field, female. **A.** Cf. *Medmassa* THA (Corinnidae), left PMS. **B.** Same, detail of Cy spigot. **C.** *Brachyphaea* cf. *simoni* (Corinnidae). **D.** *Oedignatha* cf. *jocquei* (Liocranidae) female. **E.** *Phrurolithus festivus* (Phrurolithidae) female, right PMS. **F.** *Tachelopachys ammobates* (Trachelidae) female, left. **G.** *Meriola barrosi* (Trachelidae) female left. **H.** Same, penultimate female, showing small Cy spigots.

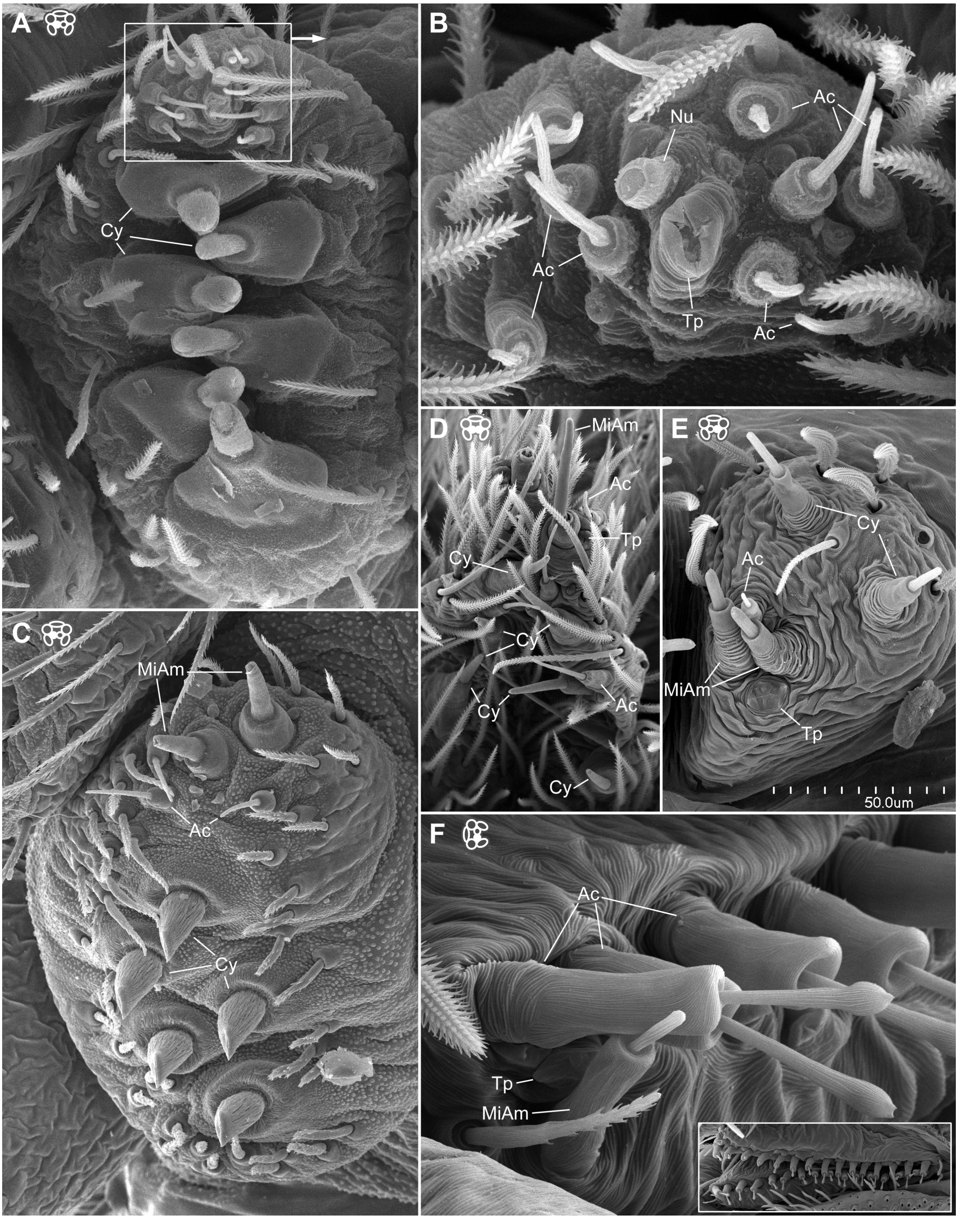

A
Cy
B
Nu
Ac
Tp
C
MiAm
Ac
Cy
D
MiAm
Ac
Tp
Cy
E
Cy
Ac
MiAm
Tp
50.0um
F
Ac
Tp
MiAm

Fig. 134. PMS spinning field. **A.** *Xenoplectus* sp. ("Gnaphosidae") female, right. **B.** Same, detail of anterior sector of left PMS. **C.** *Trachycosmus sculptilis* (Trochanteriidae) female, right. **D.** *Liocranum rupicola* (Liocranidae) female, both PMS. **E.** *Neozimiris pubescens* (Prodidomidae) male. **F.** *Prodidomus redikorzevi* (Prodidomidae) male, detail of anterior sector of right PMS, inset showing both PMS.

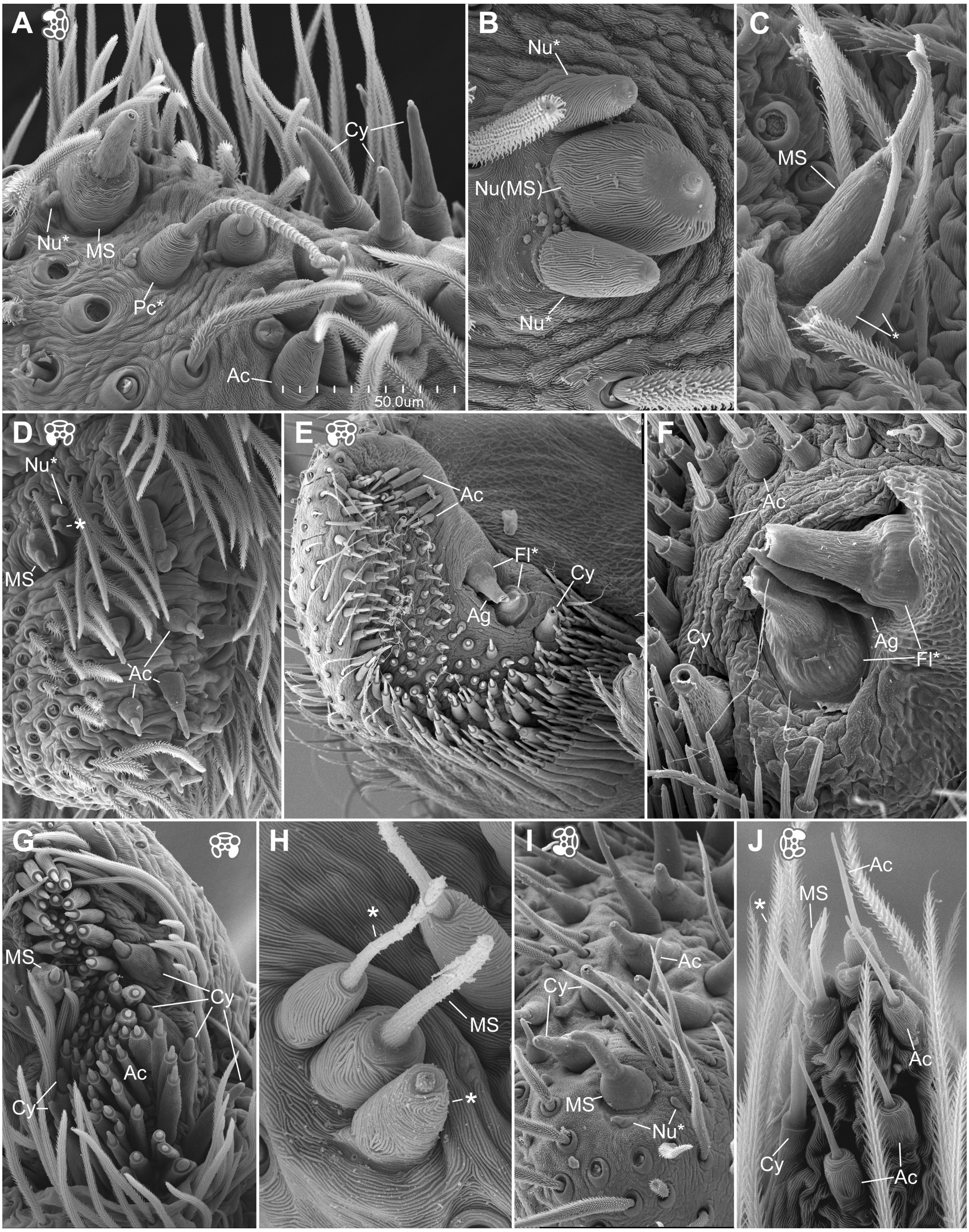

A
Cy
Nu*
MS
Pc*
Ac
50.0um
B
Nu*
Nu(MS)
Nu*
C
MS
*
D
Nu*
*
MS
Ac
E
Ac
Fl*
Cy
Ag
F
Ac
Cy
Ag
Fl*
G
MS
Cy
Ac
Cy
H
*
MS
*
I
Ac
Cy
MS
Nu*
J
Ac
*
MS
Ac
Cy
Ac

Fig. 135. PLS spinning field. Asterisks to flanking spigots or nubbins of the PLS triad. **A.** *Thaida peculiaris* (Austrochilidae) female, right PLS, detail of apical spigots. **B.** *Tengella radiata* (Tengellidae) male right, detail of triad. **C.** *Stegodyphus mimosarum* (Eresidae) female right, detail of triad. **D.** *Eresus* cf. *kollari* (Eresidae) male right. **E.** *Araneus* sp. (Araneidae) female right. **F.** Same, deatil of triad. **G.** *Uloborus glomosus* (Uloboridae) female left. **H.** *Pimus napa* (Amaurobiidae) female right, detail of triad. **I.** *Psechrus argentatus* (Psechridae) female left. **J.** *Ciniflella* ARG (Tengellidae) female left.

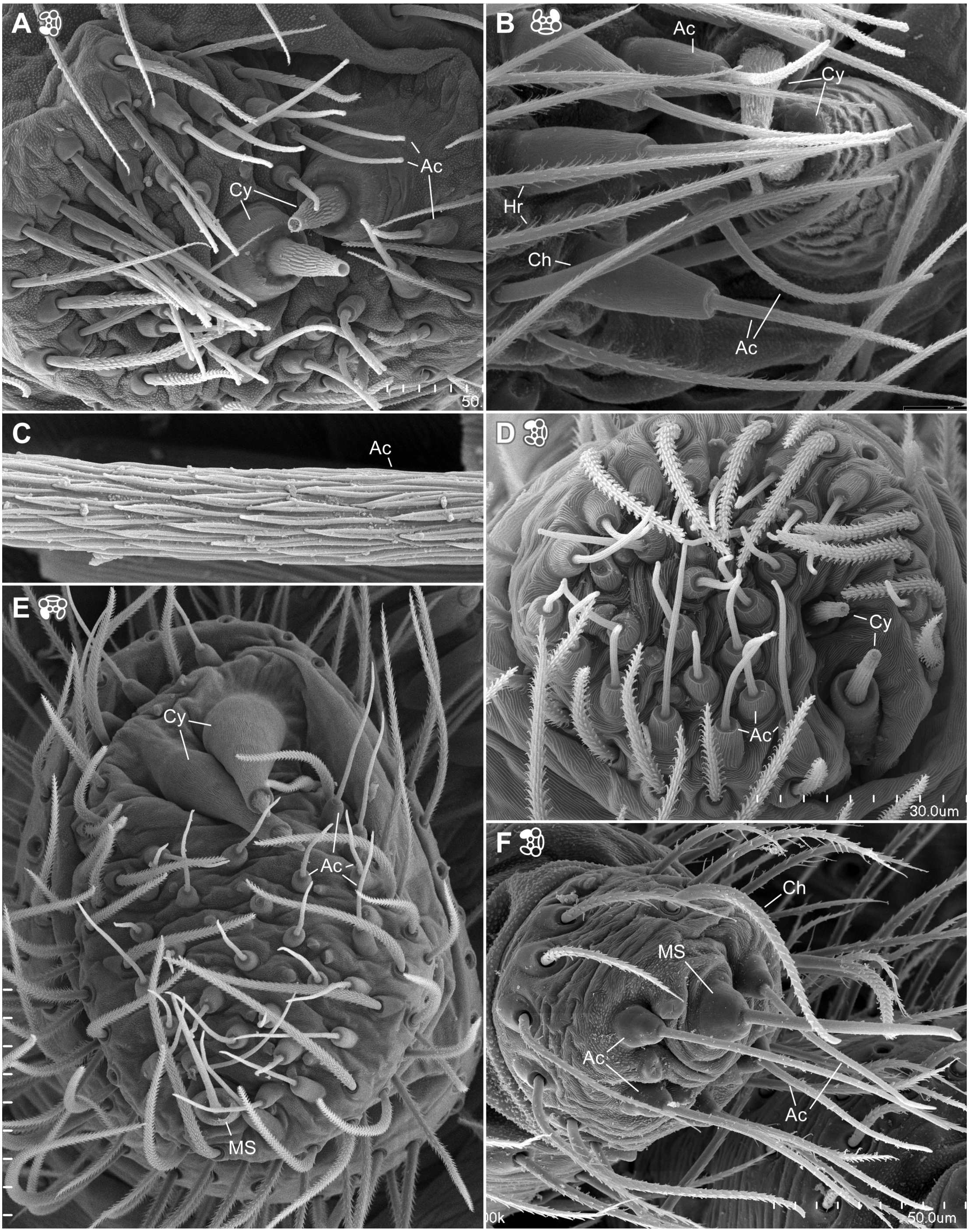

A
Ac
Cy
50.
B
Ac
Cy
Hr
Ch
Ac
C
Ac
D
Cy
Ac
30.0um
E
Cy
Ac
MS
F
Ch
MS
Ac
Ac
0k
50.0um

Fig. 136. PLS spinning field and spigots. **A.** *Corinna bulbula* (Corinnidae) female. **B.** *Falconina gracilis* (Corinnidae) female. **C.** *Systaria* sp. (Miturgidae) male, detail of shaft of aciniform spigot. **D.** *Hortipes merwei* ("Corinnidae") female. **E.** *Toxoniella* sp. (Liocranidae) female. **F.** *Sesieutes* sp. (Liocranidae) male.

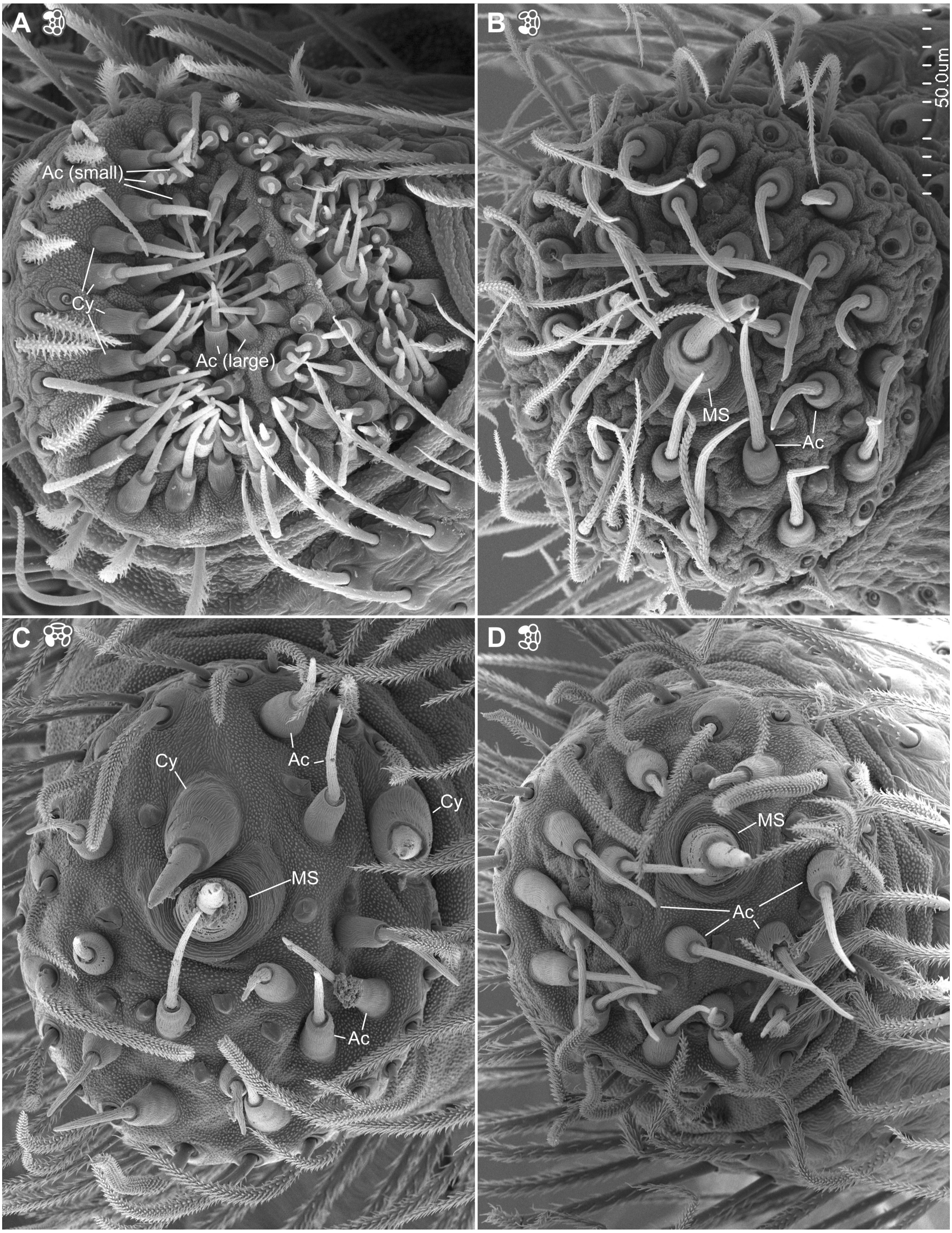

A
Ac (small)
Cy
Ac (large)
B
50.0um
MS
Ac
C
Cy
Ac
Cy
MS
Ac
D
MS
Ac

Fig. 137. PLS spinning field. **A.** *Strophius albofasciatus* (Thomisidae) female. **B.** *Cithaeron delimbatus* (Cithaeronidae) female. **C.** *Paccius* cf. *scharffi* (Trachelidae) female. **D.** Same, male.

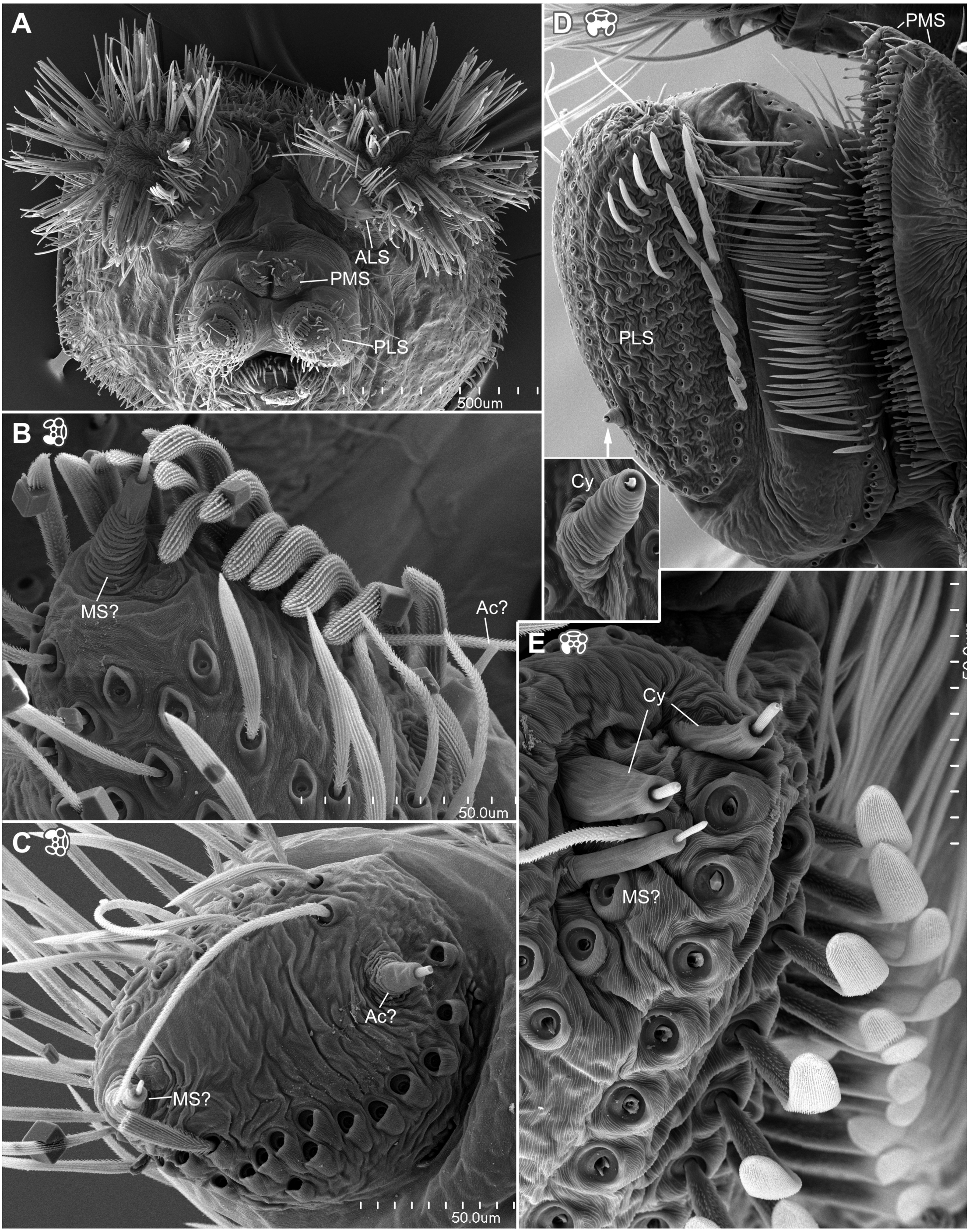

A
ALS
PMS
PLS
500um
B
MS?
Ac?
50.0um
C
Ac?
MS?
50.0um
D
PMS
PLS
Cy
E
Cy
MS?

Fig. 138. Spinnerets of Prodidominae, female. **A.** *Neozimiris pubescens* (Prodidomidae). **B.** Same, PLS. **C.** Same, PLS, thick setae removed. **D.** *Prodidomus redikorzevi*, inset to spigot on PLS. **E.** Same, anterior sector of PLS.

totally fused in Opisthothelae (Millot, 1936). The anal tubercle is the last abdominal segment (the segment 17, or abdominal segment 11), and has a tergite and a sternite, with the anus in between (fig. 109A). Spiders lack the telson (Millot, 1949).

229. Cribellum: 0. Present. 1. Absent. COMMENTS: *Stegodyphus*, *Megadictyna*, *Titanoeca*, *Dictyna*, *Neoramia*, *Stiphidion*, *Metaltella*, *Badumna*, *Psechrus*: spinneret data from (Griswold et al., 2005). *Desognaphosa*: spinnerets from Platnick (2002).

230. Cribellum spinning field division: 0. Entire. The spigots cover the entire cribellar surface in an entire spinning field (fig. 108B, D). 1. Divided. The spigots leave a bare median band, making two separate spinning fields, one at each side (figs. 111E, 112A–C, 112E).

231. Cribellum base division: 0. Entire or slightly notched (figs. 108B, D, 111E, 112A). 1. Well divided in two lobes by a longitudinal furrow (fig. 112C, E).

232. Cribellar spigots: 0. Uniformly distributed (fig. 109C). 1. Clumped. The cribellar spigots are grouped into tightly packed groups surrounded by bare cuticle (fig. 112E, F). COMMENTS: *Zoropsis*: the transverse series are here considered clumps (scored 1).

233. Clumps of cribellate spigots: 0. Entire transverse series (fig. 112C, D). 1. Transverse series of longitudinal segments (fig. 112E, F). 2. Spots. The clumps are small spots uniformly distributed (Griswold et al., 2005: fig. 97D, E). This state occurs in the zorocratid *Uduba*, not in this dataset.

234. Cribellum spigot morphology: 0. Strobilate. The spigots are thin, with evenly spaced annular expansions (fig. 109B). 1. Claviform. The spigots are expanded at the tip, and the annular ridges are superficial (fig. 111F). This is typical of filistatids.

234. Cribellar spigots surrounding cuticle: 0. With ridges. The cuticle between cribellar spigots has a sculpture of ridges (fig. 109C, D). 1. Smooth. The cuticle between cribellar spigots is smooth (fig. 109E). COMMENTS: *Zoropsis*: too closely packed (scored -). *Acanthoctenus*: one circular ridge surrounding each spigot (scored 0).

236. Cribellum development, first spigots: 0. Many small spigots without base (figs. 108A, 111A, C, D), and small calamistrum. 1. Two large spigots with base (fig. 108C), without calamistrum. In filistatids and *Hypochilus*, the first spigots to appear in the cribellum are identical to the regular cribellar spigots, of minute size and without a base (figs. 108A, 110A–C, 111B–D), and the spiderlings of this stage have a small calamistrum with setae similar as in the adult. In Austrochilines and the hypochilid *Ectatosticta*, the first cribellar spigots are two large spigots with base, similar to those of spinnerets, two to three times larger than the regular cribellar spigots found in later stages (figs. 108C, 110D–H); in these cases the spiderlings lack a calamistrum. COMMENTS: *Thaida*: scored from *Austrochilus forsteri* (scored 1).

237. Colulus: 0. Well-defined lobe (includes cribellum) (fig. 116D). 1. Hairy plate (median or paired) or two setae (fig. 108F). 2. Absent (fig. 115D). States are ordered. Cribellates are scored State 0, because the homology of the colulus with the cribellum is clear. It is often unclear whether there are one or two hairy plates, hence these conditions are not discriminated. COMMENTS: *Macrobunus*: dorsal side sclerotized (scored 0). Cf. *Medmassa* THA: large hairy plate (scored 1). *Teutamus*: two setae each side (scored 1). *Phrurotimpus*: two setae seen in male (scored 1). Cf. Gnaphosoidea TEX: two setae (scored 1). *Polybetes*: a sclerotized pit! (scored 2). *Eusparassus*: a sclerotized depression, digestion suggests that it is a muscle apodeme (scored 2). *Lessertina*: large hairy plate (scored 1).

238. Spigots insertion articulation: 0. Simple, insertion of spigots continuous with cuticle or through simple fold (figs. 116E, 124C). 1. Insertion annulate, flexible (figs. 128B, 134E, 138B). Prodidomines have most of their spigots inserted on flexible, annulate articulations. Hypochilids have a superficially similar morphology, but the annulations or squamations occur all over the spigot base (fig. 116B).

239. Tartipores: 0. Present (fig. 118H). 1. Absent. Members of Haplogynae lack tartipores (fig. 117E, G). See Griswold et al. (2005: char. 70). COMMENTS: *Hypochilus*: without tartipores, only small pores, commented on by Platnick et al. (1991: char. 63); these pores also occur in the hypochilid *Ectatosticta* (personal obs.) (scored 1). *Ariadna*: only some dubious scars in male PLS, and female PMS, but seemingly asymmetrical. Until new observations are available, I interpreted the male scar as an abnormality, and those on female PMS as foldings (scored 1). Cf. Gnaphosoidea TEX: a few can be seen on PLS (scored 0). *Xysticus*: those of PLS small (scored 0).

240. Spigot shaft surface: 0. Longitudinally ridged (fig. 123F). 1. Annulate. This is characteristic of filistatids (fig. 117F). 2. Smooth (fig. 118E). Sometimes only some spigots have sculpture while the rest are smooth; in that case I scored this character from the sculptured spigots. Griswold et al. (2005: char. 70) scored this character from ampullates only. Comments: *Ariadna*: Slightly irregular, mostly smooth (scored 2). *Storenomorpha*: Ridged only on cylindricals, the rest smooth (scored 0). *Paradiestus*: although major ampullates with smooth shafts (scored 0). Cf. Gnaphosoidea TEX: longitudinally ridged on PMS and PLS (scored 0). *Polybetes*, *Eusparassus*: some with weak longitudinal ridges, but mostly smooth (scored 02).

241. Anterior lateral spinnerets (ALS): 0. Present. 1. Absent. All terminals in this dataset have ALS. The loss of the ALS is characteristic of many Mygalomorphae.

242. ALS anteroposterior position: 0. Close to PMS and PLS. 1. Advanced far from PMS and PLS (fig. 115E). Prodidomids of the subfamily Molycriinae (not in this dataset) have the ALS far advanced, separated by pilose cuticle from the posterior spinnerets (Platnick and Baehr, 2006: figs. 12–17, 242, 243). These authors mention the synanthropic prodidomine genus *Zimiris* as the only other gnaphosoid sharing this character (see also Platnick and Penney, 2004).

243. ALS separation: 0. Contiguous to slightly separated (figs. 114D, 115B). 1. Separate about one ALS diameter or more. Gnaphosoids (fig. 115F) and cribellate taxa (fig. 106B) often have well-separated ALS. Several terminals with intermediate separations are scored as ambiguous (fig. 115C). COMMENTS: *Huttonia*: slightly less than a diameter (scored 01). *Cyrioctea*: almost a diameter, thin ALS (scored 01). *Pseudocorinna*, *Drassinella*, *Hovops*, *Anyphops*: slightly separated (scored 0).

244. Specialized setae on ALS basal article: 0. None. 1. Mesal row of thick setae. Typical of the subfamily Filistatinae (Filistatidae) (fig. 117B, C). 2. Anterior bunch of thick setae in males. This condition occurs convergently at least in males of *Zora* (Miturgidae) and both sexes of *Arachosia* (Anyphaenidae; Ramírez, 2003) (fig. 114A, B).

245. ALS basal article crossed by diagonal membranous area: 0. Absent. Basal article entire (fig. 114D). 1. Present. Basal article crossed by a diagonal membranous area (fig. 116D). This character has been reported by Simon (1893: 310) and is seemingly a synapomorphy of Dysderoidea, as it is present at least in *Trogloraptor* (Trogloraptoridae) (Griswold et al., 2012), *Dysdera* (Dysderidae), *Ariadna* (Segestriidae), several genera of Oonopidae and *Orsolobus* (Orsolobidae) (personal obs.; Matías Izquierdo, personal commun.). Caponiidae, the reputed sister group of the Dysderoidea (see Ramírez, 2000) has an entire, two-segmented ALS without membranous area (Platnick et al., 1991: figs. 145, 150).

246. ALS intermediate article: 0. Present, incomplete lateral ring. Primitive Araneomorphae retain the intermediate ALS article as an incomplete lateral ring (figs. 117A, 118A). 1. Absent (fig. 115A). COMMENTS: *Polybetes*: probably because of desclerotization of the basal article (i.e., internal side not sclerotized) (scored 0).

247. ALS distal article at ectal margin: 0. External margin entire. The distal article of the ALS is usually semilunate, mesally open in the major ampullates area. In most spiders the distal article is entire, with a continuous distal margin (figs. 121B, 126D). The sclerotization of the article is best seen with incident light in the stereomicroscope, but can also be inferred in SEM images by the setae insertions, as setal sockets occur only on sclerotized cuticle. 1. External margin interrupted. In higher gnaphosoids the distal article of the ALS is reduced, broken into relictual isolated patches with setae sockets, with at least the external margin interrupted (fig. 126B, E). The only remaining setae belonging to the distal article may be present just around the major ampullate gland spigot area (fig. 129B). In prodidomids the external margin is interpreted as being reduced to the isolated patches of setae at the base of each piriform spigot (fig. 128B). This character was scored here in a broader sense than the original use by Platnick (2002: char. 3). Here the isolated setal sockets of gnaphosoids such as *Cithaeron* (fig. 126E) and *Platyoides* (fig. 126B) are considered as interrupted ALS ectal margins. COMMENTS: *Xenoplectus*: SEM defective in male, I only see the setae (scored 0).

248. ALS major ampullate gland spigots: 0. Absent. 1. Present. Present in all terminals in this dataset. COMMENTS: *Homalonychus*: specimen with preparation MJR-562 did not spin a dragline, even when falling (scored 1).

249. Ampullate spigot shafts papillate: 0. Absent. The surface is smooth or slightly striated. 1. Present (fig. 131A) (Griswold et al., 2005: char. 68, state 1). Some corinnids have similarly papillate shafts in the cylindrical gland spigots figs. 133B, 136A). COMMENTS: *Corinna*, *Castianeira*: with some papillae, not so markedly as in eresids, but mainly on cylindricals (scored 0).

250. Major ampullate and aciniform shafts shape: 0. Shafts cylindrical or tapering. 1. Shafts clavate, widened at the tip (figs. 128D, 134F).

251. Position of major ampullates relative to piriform field: 0. Only marginal cluster of major ampullate spigots. The major ampullates are placed only on the *major ampullate field*, a definite patch usually on the mesal margin of the ALS spinning field (fig. 116A, C), placing the ampullate spigots from both sides closer together, seemingly to help make a coherent dragline. The cuticle of the major ampullate field is smoother, more sclerotized than the piriform field, and usually has several sensilla (fig. 106E; Gorb and Barth, 1996). These sensilla assist in the identification of major ampullates in drastically modified patterns of spigots, e.g., when the piriforms are absent (fig. 126H) or highly modified, or the major ampullates are reduced. See also character 255 for a further modification of the major ampullate field. 1. Marginal cluster of major ampullates, plus some major ampullates dispersed among piriforms. Some of the relatively basal Araneomorphae (filistatids, eresids) have, in addition to a mesal marginal cluster, one or more major ampullates whithin the piriform field (fig. 117D, E, H, I). COMMENT: *Oedignatha*: there is a larger piriform close to the major ampullates (scored 0). *Galianoella*, *Ammoxenus*: piriforms absent (scored -).

252. Major ampullates, general number: 0. Three or more (fig. 116B). 1. Two or less. Most Araneomorphae have a consistent pattern of only two major ampullate spigots segregated on the mesal major ampullate field (figs. 106E, 118B). After reaching maturity, one of them may be replaced by a posterior nubbin (see char. 253 below). The ontogeny of these two spigots is well known for *Araneus* (Tillinghast and Townley, 1994; Townley and Tillinghast, 2003). See also Griswold et al. (2005: char. 58). COMMENTS: *Hypochilus*: Two large plus several small major ampullates, similar to a piriform spigot (scored 0).

253. Major ampullates, number in female: 0. Two (generally with a major ampullate tartipore visible) (fig. 106E). 1. One plus a nubbin (generally with a major ampullate tartipore visible) (figs. 118B, 123E). 2. One, no nubbin (there may be a major ampullate tartipore) (figs. 116E, 125C). This infrequent condition is scattered in several families. In *Desis*, there are traces of what might be a very shallow nubbin (fig. 118E). Several Phrurolithidae in this dataset have only one major ampullate spigot without nubbin, but some closer relatives have a very small posterior major ampullate (see char. 254 below). States are ordered. This character was considered not applicable for a few terminals with more than two major ampullates (see char. 252 above). A previous character version also scored for the presence of a major ampullate tartipore; as can be seen from the comments below, the identification of such a tartipore is very often contentious. COMMENTS: *Eriauchenius*: The nubbin is not smooth. Immature has two major ampullates (scored 1). *Cybaeodamus*: tartipore not seen but area crowded (scored 0). *Medmassa*: female observed with stereo, spigots visible (scored 0). *Pronophaea*: nubbin very small, visible on left spinneret (scored 1). *Olbus*: stereomicroscope, plus Ramírez et al. (2001: figs. 11–13) (scored 0). *Apostenus*: clumped, tartipore might be hidden (scored 0). *Liocranum*: very small nubbin (scored 1). *Toxoniella*: major ampullate small, distinguishable by sensilla (scored 0). *Otacilia*: the anterior major ampullates very large (scored 0).

Hortipes: very small nubbin (scored 1). *Teutamus*: tartipore not visble but shrunken cuticle (scored 0). *Hortipes*: very small nubbin (scored 12). *Oedignatha*: one is smaller, and more central (scored 0). *Prodidomus*: the tartipore might be between the major ampullates article and the piriform field (see *Gnaphosa*) (scored 0). Cf. Gnaphosoidea TEX: the tartipore might be between the major ampullates article and the piriform field (scored 2). *Lampona*: female tartipore on border of piriform field (scored 0). *Ammoxenus*: tartipore not seen, but area not well exposed (scored 0). *Cithaeron*: the tartipore might be in the furow between piriforms and major ampullate fields (scored 0). *Gayenna*: I cannot see a tartipore in male, dubious in female (scored 0). *Systaria*: tartipore not seen, poor preparation (scored 0). *Strotarchus*: I cannot see the tartipore (scored 1). *Griswoldia*: tartipore visible in *G. urbense* (Griswold, 1991) (scored 0). *Ciniflella* BRA: perhaps a tartipore hidden by the piriforms (scored 0). *Boliscus*: tartipore not seen, dirty preparation, major ampullate spigots scored from subadult female (no major ampullate reduction in adult females seen in other thomisids) (scored 0). *Thomisus*: dirty preparation (scored 0). *Plexippus*: left side two plus tartipore (scored 01).

254. Female major ampullate shaft sizes: 0. Anterior much smaller than posterior (figs. 123B, 124B, 127F). 1. Both similar size (fig. 123A). The posterior major ampullate can be slightly smaller (fig. 123F), but I distinguished only large size differences. The posterior major ampullate or its corresponding nubbin often embraces the base of the anterior major ampullate. 2. Anterior very thick, posterior thin (fig. 125A, E). States are ordered. COMMENTS: *Eriauchenius*: immature similar sizes (scored ?). *Homalonychus*: posterior is external when invaginated (see also male nubbin) (scored 1). *Phrurotimpus*, *Drassinella*, *Orthobula*, *Neozimiris*: only one (scored ?). *Neato*: the bases are slightly different, the shafts less so (Platnick, 2002: figs. 47–52) (scored 1). Miturgidae QLD: poor preparation (scored ?). *Xenoplectus*: Anterior slightly larger (scored 1). Cf. Eutichuridae QLD: broken, but enough for scoring (scored 1). *Ciniflella* BRA: posterior slightly smaller (scored 1). *Titanebo*: posterior major ampullate slightly smaller (scored 1). *Plexippus*: left side has two, similar size (scored 1).

255. Female major ampullate field invagination: 0. Marginal field (fig. 123F). 1. Central invaginated field, transverse line. One of the major ampullate spigots is marginal, the other more central (figs. 119A, F, 123B). 2. Central invaginated field, longitudinal line. Both major ampullates are far from the margin of the spinning field (fig. 119B–D). States are ordered, as the transverse line has one of the major ampullates still in marginal position. This character was conceived as applicable only to the stereotyped pattern of one or two major ampullates in a definite major ampullate field (see chars. 251 and 252). The furrow or wrinkles delimiting the major ampullate field, as well as its sensilla, indicates that this is the marginal major ampullate field that has been invaginated, rather than that the major ampullate is within the piriform field, as in character 251. State 2 is a synapomorphy of Zodariidae, with a remarkable convergence in the zoropsid *Uliodon* (see Miller et al., 2010). COMMENTS: *Hypochilus*: the two large ones might still be homologous to the marginal ones (scored -). *Stegodyphus*: one of the two large marginal major ampullates is out of the sensila field (scored -). *Desis*: Only one (scored ?). *Cryptothele*: adult female with nubbin and major ampullate in transverse line (fig. 119E), immature with two major ampullates in same positions (fig. 119F), both cases with marginal tartipore (scored 1). *Homalonychus*: posterior one is external when invaginated (see also male nubbin) (scored 1). *Oedignatha*: one marginal one central, also observed in several other species, including larger ones from India (scored 1). *Galianoella*: no piriforms (scored 02). *Ammoxenus*: piriforms absent, major ampullates in oblique line (scored ?).

256. Major ampullate field on anterior margin: 0. On mesal margin (fig. 116C). 1. On anterior margin (figs. 118A, D, 121C, D). This character has been proposed by Davies (Davies, 1999: char. 20). COMMENTS: *Desis*: definitely anterior (scored 1). *Camillina*, *Austrachelas*, *Lessertina*: intermediate (scored 01). *Ammoxenus*: piriforms absent (scored ?).

257. Major ampullate field projection: 0. Major ampullate field on a flat (fig. 123F) or slightly domed area (figs. 126A, 127F, 128F, G, 129D–F). 1. MAmp field on a conical, well-defined, setae-bearing article (figs. 127D, 128B, E). The conical article found in some prodidomids seems an extreme of the trend found in other gnaphosoids of having the major ampullate field on a domed area. There are many intermediate conditions for a reliable scoring of such a subtly elevated area. It is not clear where the major ampullate tartipore or nubbin is placed in prodidomids with a conical article. In terminals with a domed major ampullate field, the major ampullate tartipore stays in the furrow between the major ampullate and piriform fields, but the nubbin stays on the major ampullate field (fig. 129F) and the major ampullate sensilla are still present (fig. 129E). COMMENTS: *Neozimiris*: Platnick (1990: 37) referred to the fusion of the major ampullate field projection with the ALS basal article, not observed in this specimen (fig. 128B) (scored 1).

258. Major ampullates, number in male: 0. Two (generally with a major ampullate tartipore visible). 1. One plus a nubbin (generally with a major ampullate tartipore visible). 2. One, no nubbin (there may be a major ampullate tartipore). States are ordered. Same as character 253, but for the male. COMMENTS: *Uloborus*: male after *Waitkera* from Platnick et al. (1991) (scored ?). *Cybaeodamus*: tartipore not seen, but poorly preserved (scored 0). Cf. *Medmassa* THA: male spigots seen in stereomicroscope (scored 1). *Mandaneta*: I cannot see the tartipore with the stereomicroscope (scored 1). Cf. Liocranidae LIB: tartipore not seen (scored 1). *Hortipes*: very small nubbin (scored 1). *Oedignatha*: the more central major ampullate is smaller, similar to a piriform spigot (scored 0). Cf. Gnaphosoidea TEX: only one, tartipore or nubbin not seen at this magnification from KOH digested specimen, needs SEM confirmation (scored 12). *Meedo*: one is broken (scored 0). *Trachycosmus*: male tartipore is marginal! (scored 0). *Fissarena*: tartipore not seen (scored 0). *Malenella*: male spinnerets not scanned (scored ?). *Amaurobioides*: in stereomicroscope, tartipore not seen (scored 1). *Lessertina*: small nubbin as in female (scored 1). Miturgidae QLD: I cannot see a nubbin, all piriforms hiding details (scored 12). *Griswoldia*: male spinnerets from from *G. urbense* (Griswold, 1991: figs: 37–40) (scored 1). *Hovops*: males observed with stereomicroscope (scored 1). *Boliscus*: nubbin or tartipore not seen, dirty preparation (scored 12). *Xysticus*: small nubbin (scored 1). *Plexippus*: dirty preparation, I cannot see the tartipore (scored 1).

259. Piriform gland spigots in adults: 0. Present (figs. 118B, 125A). 1. Absent (fig. 126C, D).

260. Piriform bases reduced: 0. Absent. Spigot base well defined from surrounding cuticle (fig. 125A). 1. Present. Spigot base not well defined, very short (figs. 116F, 118B). COMMENTS: *Huttonia*: all spigot bases reduced (scored 1). *Ammoxenus*: piriforms absent (scored ?).

261. Piriform spigot base cuticle texture: 0. Longitudinal ridges (fig. 123F). 1. Concentric ridges (fig. 118F). 2. Smooth (fig. 119F). 3. Annulate-squamate as in Hypochilidae (fig. 116B). COMMENTS: *Oecobius*: smooth (scored ?). *Araneus*: weak but present (scored 0). *Desis*: somewhat mixed (scored 1). *Macrobunus*: wavy, more often annulate (scored 01). *Homalonychus*: smooth (scored 2). *Teutamus*: some with very faint ridges (scored 02). *Prodidomus*: some spigots with annular ridges on PMS and PLS (scored 0). *Lygromma*: concentric waves (scored 2). *Ammoxenus*: piriforms absent (scored ?). *Cheiracanthium*: very faint (scored 0). *Syspira*: smooth (scored 2). *Ciniflella* BRA: waving (scored 01). Sparianthinae VEN: smooth (scored 2). *Heteropoda*: not enough magnification in SEM images (scored ?). *Polybetes*: very weak longitudinal (scored 02).

262. Female piriform shaft thickness relative to major ampullate shaft: 0. Piriform shaft thinner, or equal as in major ampullate (figs. 123F, 124E). 1. Piriform shaft thicker than in major ampullate (figs. 127F, 129A). In some terminals one of the major ampullates is reduced (see char. 254), in those cases this character is scored after the larger major ampullate (fig. 124E). COMMENTS: *Cyrioctea*: longer (scored 0). *Homalonychus*: larger major ampullates in female, but male has small major ampullates (scored 0). *Apostenus*: piriforms rather thick, but only thicker than the smaller of the two major ampullates (scored 0). Cf. Liocranidae LIB, *Pseudolam-*

pona: equal (scored 0). *Gnaphosa*: an equal number of piriforms and corresponding tartipores suggests that all piriforms are functional during molt (scored 1). *Lygromma*: very long piriform bases, but small shafts (scored 0). *Lamponella*: piriforms smaller than the larger major ampullate (scored 0). *Doliomalus*: about the same, all thick (scored 0). *Cithaeron*: about the same size (scored 0). *Miturga gilva*: the marginal piriforms larger in male (scored 0). *Syspira*: shaft thinner, only larger in male (scored 0). *Odo bruchi*: quite large (scored 0).

263. Piriform shaft-base transition: 0. Transition with a well-defined change in curvature (figs. 123C, D, 129H, J). 1. Transition on a continuous curvature, only a superficial marking (fig. 129A, G). COMMENTS: *Ariadna*: slightly separate (scored 0). *Storenomorpha*: not sharply delimited (scored 0). *Clubiona*: well defined also in male (scored 0).

264. Demarcation between major ampullate and piriform fields: 0. Major ampullate field integrated with piriform field, or separated only by flat cuticle or wrinkles (figs. 116C, 123F). 1. Separated by deep furrow only in male (fig. 121A). 2. Separated by a deep furrow in male and female. The major ampullate field is well delimited from the piriform field by a deep furrow (figs. 118C, 124A, 126E, 129C). States are unordered; the distribution of the males-only demarcation does not suggest intermediacy. The furrow delimits well-separated major ampullate and piriform fields, sometimes in conjunction with a great development of the piriform field. COMMENTS: *Huttonia*, *Psechrus*, *Ciniflella* BRA: superficial wrinkles (scored 0). *Clubiona*: superficial wrinkles in female (scored 1). *Xenoplectus*: not so markedly (scored 2). *Phrurotimpus*, *Hortipes*, *Trachycosmus*: intermediate, slightly marked separation in female (scored 012). Cf. Gnaphosoidea TEX: female from SEM, male from KOH digested specimen (scored 2). *Titanebo*, *Polybetes*, *Eusparassus*: major ampullate field depressed (scored 0).

265. Male separate major ampullate field with smaller piriforms: 0. Separate field only with major ampullates (fig. 125F). 1. Some small piriforms with the major ampullates (figs. 120C, D, 124G). This character was considered applicable only to terminals with major ampullate and piriform fields well delimited by a deep furrow. The piriform spigots on the major ampullate field are of similar shape as those of the female. COMMENTS: *Clubiona*, *Elaver*, *Agroeca*: well defined in male (scored 1).

266. Piriform spigots size sexual dimorphism: 0. About same size in male and female (compare fig. 121E, F). 1. Male piriforms larger (compare fig. 122D, F). For those terminals with two sizes of piriforms (see chars. 265 and 267), the ectal and more numerous piriforms are used to score this character. COMMENTS: *Agroeca*: I am scoring the ones in the main piriform field (there are smaller piriforms together with the major ampullates) (scored 1). *Apostenus*: male with only one piriform, in fact relatively smaller than those on female (scored 0). *Doliomalus*: male with slightly longer shafts (scored 0). *Miturga gilva*, *Systaria*: slightly so (scored 1). *Miturga* cf. *lineata*: slightly larger in male, especially ectal ones (socred 1). *Syspira*: very slightly larger, especially the ectal ones (scored 01). *Odo bruchi*: perhaps slightly larger in female than in male (scored 0). *Ciniflella* ARG: ectal piriforms slightly larger than in female (scored 1). *Ciniflella* BRA: at least the four ectal piriforms larger (scored 1).

267. Male piriforms enlargement in mesal sector: 0. All male piriforms larger than in female (fig. 122B). 1. Mesal piriforms closer to the major ampullates smaller than the rest, similar as in the female. This includes the small piriforms in the separate major ampullate field (char. 265).

268. ALS basal article cylindrical, with inflatable piriform field: 0. Absent, ALS a truncate cone (fig. 113B) or near cylindrical, but not inflated (fig. 113C). 1. Present in males. The ALS are large, cylindrical to wider distally, and the piriform field can be considerably inflated (figs. 120A, B, 122A, 124F). 2. Present in males and females (figs. 115G, 127A, 128A, 129B, C). States are ordered, because the sexually dimorphic condition is found in several taxa and seems a plausible intermediate for the morphology found in gnaphosids and prodidomids. The cylindrical ALS basal article occurs in conjunction with a modified piriform field. It is remarkable how this syndrome appears in clubionids, gnaphosoids, liocranids, and miturgines, some of which are distantly related. The inflatable piriform field seems to be a mechanism to expose and retract the enlarged piriform spigots (compare figs. 127A, 129C). This character is related with the absence of a distal segment on ALS, and enlarged piriforms (see chars. 247, 262 and 266); some terminals with inflated piriform field but not cylindrical ALS were scored absent for this character. COMMENTS: *Xenoplectus*: piriform field somewhat inflated but not cylindrical (scored 0). *Teutamus*: intermediate, in male (scored 01). *Lampona*: inflated piriform field, but not cylindrical ALS (scored 0). *Austrachelas*: inflated piriform field, but not cylindrical ALS (scored 0). *Cithaeron*: female ALS not cylindrical (scored 1). *Miturga gilva*: basal article and piriforms slightly enlarged in male (fig. 122E, C) (scored 01).

269. Piriform spigots, number configurations by sex: 0. Male and female more than three piriforms. 1. Female several piriforms, male none to three. In phrurolithids the number of piriform spigots is consistently reduced in males (compare fig. 125A–C). This also occurs in some scattered gnaphosoids and liocranids as well (e.g., fig. 124C, D). 2. Piriforms absent in male and female (fig. 126F–H). States are ordered. COMMENTS: *Trachelas minor*: female 7, male 4 (scored 0). *Xenoplectus*: female 5, male 3 (scored 1). Cf. Liocranidae LIB: male observed with compound, quite clear, 4 large piriforms (scored 0). *Orthobula*: female 7, male 3 (scored 1). *Lampona*: female several, male 5 (scored 0). Trachelidae ARG: both male and female 5 piriforms (scored 0). *Teutamus*: female many, male 3 (scored 1). *Eilica*: Female 3, male at least 1. Scored from *Eilica bicolor* female with four piriforms (Platnick, 1990: 23) (scored 0). *Micaria*: tentatively scored 1, the female has 1 piriform, and the male none (fig. 129H, I). Cf. *Moreno* ARG: male and female with 3 large piriforms (scored 0). *Austrachelas*: female about 33, male 11 (scored 0). *Vectius*: female 6, male 7 (scored 0). *Cithaeron*: female 4, male 1 (scored 1). *Pseudolampona*: male and female 1 (scored 0). *Odo bruchi*: female 8, male 5 (scored 0).

270. Central piriform spigot with plumose base: 0. Absent, base without barbs. 1. Present. Both sexes of *Lygromma* have a central piriform with barbs on its base, a morphology intermediate between spigot and seta (fig. 127E). This might be related with the occurrence of setae with a long, pore-bearing apical tube on leg and palpal tarsal tips (see char. 175), reminiscent of spigots.

271. Piriform spigots with elongate bases flanked by plumose setae: 0. Absent, the piriform bases are shorter than the shaft. 1. Present, moderately elongated bases with loosely associated setae (fig. 127F). 2. Present, extremely elongated bases closely encircled by setae. The lateral piriforms have an external arc of flanking setae (figs. 127B, C, 128B). In *Neozimiris* the medial piriforms have a complete circle of flanking setae (fig. 128B). The side of the flanking setae appressed against the spigot base is smooth (figs. 127C, 128C). States are ordered. The morphology of these piriform spigots was described by Platnick (1990, 2000: char. 25, 2002: char. 6) and Platnick et al. (2005) as a synapomorphy for Prodidomidae.

272. PMS minor ampullate gland spigots: 0. Absent (figs. 131D, 133C). In gnaphosoids the reduction in size of major ampullates seemingly occurs coordinately with the minor ampullates. In such cases the reduced minor ampullates are difficult to distinguish from aciniform spigots. 1. Present. COMMENTS: *Hypochilus*: In living specimens (thanks to Jason Bond, same as preparation MJR-863) I see consistently two darker spigots: one anterior, one median-external. These may be homologs of the ampullate spigots not different in surface morphology from the acniforms (scored 0). *Stegodyphus*: interpreted according to Griswold et al. (2005) (scored 1). *Cyrioctea*: one tentatively identified as a minor ampullate because the aciniforms on PLS have much longer shafts (scored 1). *Brachyphaea*: only aciniform and cylindrical spigots (scored 0). *Xenoplectus*: there is at least a nubbin (scored 1). *Phrurolithus*: small spigot identified as a minor ampullate because of position, proximity to tartipore and comparison with male (scored 2). Trachelidae ARG: there may be a tartipore, but not all surface exposed (scored 0). *Gnaphosa*: at least one distinguishable (scored 1). Cf.

Moreno ARG: seen in male (scored 1). *Camillina*: Platnick (1990: figs. 35–37) illustrates a female of *C. elegans*, and there seems to be a second, smaller minor ampullate (scored 2). *Vectius*: no tartipores on PMS, subadult female perhaps with one or two tartipores (scored 2). *Platyoides*: anterior minor ampullate much larger, similar to modified PLS spigot (scored 0). Cf. Gnaphosoidea TEX: only one spigot, a cylindrical (scored 0). *Ammoxenus*: from male (scored 1). *Pseudolampona*: the interpretation of PMS-PLS spigots is somewhat tentative, as there is little difference between the presumed minor ampullate, modified PLS spigot, and aciniforms (scored 1). *Titanebo*: perhaps the tartipore in the middle, not visible (scored 0). *Boliscus*: tartipore not seen, dirty preparation, minor ampullate spigots scored from subadult female (no major ampullate reduction in adult females seen in other thomisids) (scored 0).

273. Female PMS minor ampullates, number: 0. Two (fig. 132D). 1. One plus nubbin (fig. 131F). 2. One, no nubbin (fig. 133E). 3. Only one nubbin (fig. 134A, B). States are ordered. There is generally a minor ampullate tartipore visible. COMMENTS: *Nicodamus*, *Titanoeca*, *Dictyna*: from Griswold et al. (2005) (scored 2). *Cybaeodamus*: hard to distinguish (scored 01). *Homalonychus*: identified as minor ampullates because they are larger and male has nubbins instead (scored 0). *Psechrus*: tentatively identified after male nubbin (the presumable minor ampullates are similar to cylindrical gland spigots) (scored 0). *Acanthoctenus*: the large one anterior identified after the male (scored 0). *Cycloctenus*: there may be a hidden tartipore (scored 2). *Trachelas minor, Pseudocorinna, Lauricius*, *Griswoldia*, *Petrichus*: there may be a hidden tartipore (scored 0). *Procopius*: tartipore together with one of the minor ampullates in a mound (scored 0). *Olbus*: in same plate with anterior cylindrical gland spigot (scored 0). *Liocranum*: the second large spigot (from anterior) interpreted as minor ampullates because of the base not being conical (scored 0). *Phrurolithus*: small spigot identified as minor ampullate because of position, proximity to tartipore and comparison with male (scored 2). *Orthobula*: only two smaller spigots of similar size, could be interpreted as absent, or as in *Phrurolithus* (one minor ampullate) (scored ?). *Anagraphis*: not clean preparation; I can see the minor ampullates but not the tartipore (scored 0). *Gnaphosa*: identified tentatively as a minor ampullate and a tartipore, from *G. sericata* and *G. taurica* (scored 0). *Prodidomus*: There are some tartipores, perhaps of aciniform spigots. Interpreted differently from *Neozimiris*; here the minor ampullates are smaller than the aciniforms (scored 2). *Meedo*: interpreted from Platnick (2002: fig. 44) (scored 2). *Trachycosmus*: tartipore visible in male (scored 0). *Fissarena*: all very similar, not clean, at least one minor ampullate in the female, with large base (scored 02). *Amaurobioides*: many small tartipores, perhaps all of aciniforms (scored 2). *Miturga* cf. *lineata*: the second minor ampullate not individuated, but present in male (scored 02). Miturgidae QLD: poor preparation (scored ?). *Zora*: differing in the two specimens scanned (scored 01). *Xenoctenus*: only one seen, coded like this because any of the cylindricals might be a minor ampullate instead (scored 02). *Cebrenninus*: not very clear, though (scored 0). *Cocalodes*: perhaps the tartipore hidden close to the large minor ampullate (scored 0). *Lyssomanes*: the anterior minor ampullate might be a large aciniform instead (scored 02).

274. Male PMS minor ampullates, number: 0. Two. 1. One plus nubbin. 2. One, no nubbin. 3. Only a nubbin plus tartipore. 4. Only a large tartipore. Males of titanoecids have a large tartipore as the only putative remnant of minor ampullate spigots (Griswold et al., 2005). States are ordered. In states 0–2 there is generally a minor ampullate tartipore visible. COMMENTS: *Cybaeodamus*: one plus nubbin? (scored 1). *Homalonychus*: sometimes two nubbins plus tartipore (scored 3). *Acanthoctenus*: the smaller minor ampullate absent on left side! (scored 0). *Cycloctenus*: tartipore small, of an aciniform gland spigot (scored 2). *Mandaneta*: tartipore visible (scored 0). Cf. *Medmassa* THA: tartipore not seen (scored 1). *Liocranum*: Many hairs, there may be a nubbin (scored 12). Cf. Liocranidae LIB: PMS with one spigot and a mound (tartipore or nubbin?), unclear homology of the spigot (scored 1234). *Phrurolithus*: Male with one slightly larger PMS shaft, linked to a tartipore, identified as minor ampullate. The second spigot identified as aciniform. In other Phrurolithidae these two spigots are of similar size, the one not associated with the tartipore may be missing. Identified the minor ampullate in those cases by their position besides the tartipore (scored 2). *Phrurotimpus*: very small (scored 2). *Drassinella*: minor ampullate, if present, equal to the aciniform gland spigot (scored ?). *Teutamus*: tartipore visible only on right side (scored 2). *Anagraphis*: not clean preparation (scored 1). *Prodidomus*: there are some tartipores, perhaps of aciniform gland spigots (scored 2). Cf. Gnaphosoidea TEX: from KOH digested male, it only shows a sclerotized scar (scored 4). *Doliomalus*: tartipore not seen, shrunken (scored 0). *Amaurobioides*: stereomicroscope, tartipore not seen (scored 2). *Lessertina*: bad preparation, but all the same as in female (scored 2). Miturgidae QLD: tentative interpretation (scored 1). *Griswoldia*: scored from image from Diana Silva Dávila (scored 1). *Hovops*: males observed with stereomicroscope, tartipore not seen (scored 1). *Geraesta*: tartipore not seen, may be hidden (scored 1). *Xysticus*: *X. audax* with a nubbin as well (E. Jantscher, personal commun.) (scored 2). *Cocalodes*: perhaps the tartipore hidden close to the large minor ampullate (scored 0). *Holcolaetis*, *Portia*: not good preparation, only the minor ampullate visible (scored 12). *Storenomorpha*: right side two minor ampullate, left side one (scored 012). *Apostenus*: very small minor ampullate (see sensilla at side) (scored 1). *Lyssomanes*: the anterior minor ampullate might be a large aciniform gland spigot instead (fig. 132C) (scored 02).

275. Minor ampullate on posterior median margin, posterior to the group of aciniforms: 0. Absent. The minor ampullates are not on the posterior median margin, or the aciniform gland spigots extend further behind the minor ampullates. 1. Present. The minor ampullates are on the posterior median margin, and the aciniforms are grouped anteriorly (figs. 130C, 131E, G, 132B). This is most evident on males, as in females some of the cylindrical spigots may extend in an external arc, behind the minor ampullates. COMMENTS: *Ariadna*: only two spigots (minor ampullate and aciniform) (scored 0). *Badumna*: only two aciniforms more anterior to the minor ampullates (scored 0). *Storenomorpha*: minor ampullates in a common mound with anterior cylindrical spigot; right side of male with two minor ampullates (scored 01). *Homalonychus*: Only one posterior aciniform spigot (scored 0). *Acanthoctenus*: anterior minor ampullate much larger than posterior (scored 0). *Neoanagraphis*: minor ampullate and tartipore in common mound with anterior cylindrical spigot (scored 0). Cf. Liocranidae LIB: anterior group of aciniforms, median minor ampullates, and posterior group of cylindricals (scored 0). *Eilica*, *Apodrassodes*: in the middle of anterior sector (scored 0). *Legendrena*: only two aciniforms (scored 0). *Ammoxenus*: scored from male (scored 0). *Anyphops*: the minor ampullates are very large, much larger than the major ampullates (scored 0). *Senoculus*, *Strophius*: female with external arch of cylindrical spigots, some behind the minor ampullate (scored 1). *Megadictyna*: the spigots posterior to the minor ampullates might be aciniforms or cylindricals (scored 01). *Galianoella*: aciniforms absent, but minor ampullate clearly on anterior margin (scored 0). *Macerio*: one of the the minor ampullates close to the middle of the spinning field, some aciniform spigots posterior (scored 0). *Eusparassus*: mesal (scored 0). *Borboropactus*: the minor ampullates not so definitely posterior, the aciniforms describing an external arc, some of them posterior to the minor ampullates (fig. 132A) (scored 01). *Stephanopis ditissima*: the aciniforms also extend in an external arc, in the male reaching very slightly behind the minor ampullates (scored 1). *Stephanopoides*: some of the aciniforms beyond the minor ampullates (scored 1). *Lyssomanes*: the anterior minor ampullate might be a large aciniform spigot instead (fig. 132C) (scored 01).

276. Female PMS aciniform spigots, number: 0. Four or more. 1. Two or three. 2. One (fig. 134E). 3. None (fig. 133E). States are ordered. COMMENTS: *Mimetus*: female 4 but male 3 (scored 0). *Badumna*: *B. candida* 3, *B. longinqua* 2 (scored 1). *Neoramia*, *Falconina*: 2 (scored 1). *Zoropsis*: female 5, male 3 (scored 0). *Cycloctenus*, *Toxopsiella*: many in female, 2 in male (scored 0). *Castianeira*: 11 on female, 6 on male (scored 0). *Medmassa*: female 1, male 1 or 2 (scored 2). *Trachelas* *minor*: female 6, male 4 (scored 0). *Apostenus*: left 2, right 3 (scored 1). *Liocranum*: female 3 or 4 (asymmetrical), male 4 (three posterior, one anterior) (scored 01). *Drassinella*: potential aciniforms are: 4 in female, 5 in male; this leaves at least 2 aciniforms in female, and 3 in male (scored 01). *Prodidomus*: a row of aciniforms with widened tips (scored 0). *Camillina*: 3 to 4 (scored 01). *Neato*: female 3, male 6 (scored 1). *Syspira*: Female several, male 2 (scored 0). *Xiruana*: 17–18 (scored 0). *Odo bruchi*: 7 (scored 0). *Ciniflella* ARG: Variable, 2 to 3 (scored 1). *Petrichus*: female 3, male 2 (scored 1). *Cebrenninus*: female 3, male 4 (scored 1). *Boliscus*: 15 (scored 0). *Titidius*: 3, cylindrical spigots tentatively identified by the slightly larger shaft and by not being associated with tartipores (scored 1).

277. Male PMS aciniform spigots, number: 0. Four or more. 1. Two or three. 2. One. 3. None. States are ordered. COMMENTS: *Badumna*: *B. candida* two (scored 1). *Storenomorpha*: right one, left two (scored 12). *Falconina, Petrichus*: two (scored 1). Cf. Liocranidae LIB: only one spigot, either minor ampullate or aciniform (scored 23). *Camillina*: 6 (scored 0). *Xiruana*: 5–6 (scored 0). *Odo bruchi*: 8–10 (scored 0). *Ciniflella* ARG: variable, two to three (scored 1). *Hovops*: one posterior, seen with stereomicroscope (subadult none!) (scored 2). *Boliscus*: two aciniforms plus one aciniform with double shaft, symmetrical! (scored 01). *Thomisus*: 6 (scored 0). *Lyssomanes*: the anterior minor ampullate might be a larger aciniform instead (fig. 132C) (scored 01).

278. Aciniform spigot shafts two size classes: 0. Aciniform shafts uniform. 1. Aciniforms shafts in two size classes (figs. 132C, 137A). See Griswold et al. (2005: char. 85). COMMENTS: *Eriauchenius*: only one aciniform in adult, but immature has two, same sizes (scored ?). *Phrurolithus*: only one or none (scored ?). *Jacaena*: only one (scored ?). *Neozimiris*: posterior male aciniform only slightly larger (scored 01). *Systaria*: aciniform shafts very long (scored 0). *Lauricius*: only one aciniform is slightly smaller in the female (scored 0). *Aphantochilus*: only one aciniform, basal on PLS, is slightly larger (scored 01). *Strophius:* PLS with smaller aciniforms in central area (scored 1).

279. Aciniform spigot shaft barbs: 0. Only with shallow sculpture, or smooth (fig. 133D). 1. With well defined barbs (figs. 132E, F, 136C, B).

280. Cylindrical gland spigots: 0. Absent. 1. Present. See Griswold et al. (2005: char. 86.) In this dataset (or elsewhere, as far as I know), when the cylindrical spigots are present, they occur in both PMS and PLS. Small cylindrical spigots in penultimate female were observed in *Meriola barrosi* (compare fig. 133G, H). COMMENTS: *Liocranum*: the cylindricals are present in *Liocranum* and *Mesiothelus*, contra Bosselaers and Jocqué (2002: 264) (scored 1). *Prodidomus*: three, interpreted as cylindrical spigots because the aciniforms have expanded shafts (scored 1). *Macerio*: contra Ramírez et al. (1997) (scored 1). *Strotarchus*: PMS and PLS cylindrical spigots perhaps present in *Strotarchus tropicum* (SEM images by Alexandre Bonaldo, personal commun.) (scored 0). *Philodromus*: PMS with 12 aciniform spigots in both sexes, with the same distribution (scored 0). *Epidius*: cylindrical spigots tentatively identified by the longer and somewhat thicker shaft (scored 1). *Stephanopis ditissima*: scored uncertain because although all the spigots are similar, there is a difference in the margin of the spigot base, similar as in other thomisids (e.g., *Strophius*), and the female has many more spigots than the male, on PLS and PMS (scored ?). *Stephanopoides*: slightly but consistently larger shaft than those of the aciniforms (scored 1). *Boliscus*: adult female not scanned (scored ?). *Xysticus*: Demir et al. (2008: fig. 7) illustrate the eggsac of *Xysticus pseudorectilineus*, coriaceus, flat, on a stone (scored 1). *Holcolaetis*: Wanless (1985) reported gnaphosidlike eggsacs (scored 0).

281. Cylindrical spigot shaft rotund, incised: 0. Absent. 1. Present, shaft with longitudinal incisions (Platnick and Shadab, 1993: figs. 27, 28; Griswold et al., 2005: fig. 25C, D). State 1 was proposed as a synapomorphy of Mimetinae (Platnick and Shadab, 1993). Harms and Harvey (2009) found rotund but smooth shafts in *Australomimetus* (and other unspecified genera as well), and suggest that the incised shafts may be a synapomorphy of only *Mimetus* and *Ero*. No other terminal in this dataset has similar cylindrical spigots. COMMENTS: *Mimetus*: cylindricals in PMS indented as well (scored 1).

282. PMS cylindrical spigot bases sunken: 0. Base raised from surrounding cuticle. 1. Base sunken in surrounding cuticle (fig. 132G; Bosselaers and Jocqué, 2000: fig. 7b). This is a synapomorphy of *Hortipes*. Of the pair of cylindrical spigots on PLS, the medial one is also sunken (fig. 136D).

283. PMS cylindrical gland spigots, number: 0. Many. 1. Five. 2. Four. 3. Three. 4. Two. 5. One. States are ordered. COMMENTS: *Oecobius, Dictyna*: one cylindrical, interpreted as in Griswold et al. (2005) (scored 5). *Senoculus*: Six (scored 0). *Brachyphaea*: five or six (scored 01). *Apostenus*: Identified with difficulty with reference to PLS, then the other two large spigots identified as minor ampullates (scored 5). *Liocranum*: the second large spigot, counting from anterior to posterior, interpreted as a minor ampullate (scored 3). *Xenoplectus*: six (scored 0). *Lampona*: I counted six cylindricals (scored 0). *Austrachelas*: 10 (scored 0). *Desognaphosa*: variable (scored 012). Miturgidae QLD: poor preparation, identified some cylindricals, but the minor ampullates are not clear (scored 1234). *Petrichus*: right two, left three (scored 34).

284. PMS cylindrical spigots, clustering: 0. Mixed with aciniforms or minor ampullates (fig. 131C). 1. Isolated posterior group (figs. 133F, 134C). In this dataset, when many cylindrical spigots occur in a posterior isolated group, they are aligned in longitudinal rows; there are some cases of irregular lines, but none in a clearly disorganized pattern. COMMENTS: *Oecobius*, *Cyrioctea*: only one (scored ?). *Neoramia*: few spigots, one PC close to anterior cylindrical spigot (scored 01). *Pimus*: only one, posterior (scored ?). *Meriola*, *Trachelopachys*, *Toxoniella*, *Phrurolithus*, *Phrurotimpus*, *Otacilia*, *Drassinella*, *Orthobula*, *Jacaena*, *Fissarena*, *Ammoxenus*, *Meedo*: isolated posterior group forming rows (scored 1). *Sesieutes*, *Trachycosmus*: rows not well formed (scored 1). *Centrothele*: isolated posterior group in a row (scored 1). *Lamponella*: only one, posterior (scored ?). *Austrachelas*: only a couple of aciniforms reaching anterior sector of the two cylindrical spigot rows (scored 1). *Vectius*: minor ampullate anterior, right side with one cylindrical anterior to minor ampullate (scored 01). *Griswoldia*: one of the cylindricals together with the aciniforms (scored 0).

285. PMS paracribellar spigots: 0. Absent. 1. Present (fig. 130A, E, I). COMMENTS: *Stegodyphus*: note that the triad flanking spigots have longer shafts than those of the surrounding aciniforms (Griswold et al., 2005: figs. 33J, 37D) (scored 0). *Zorocrates*: see the shaft fused to PLS modified spigot! (Griswold et al., 2005: fig. 101D) (scored 0).

286. PMS paracribellar spigots, number: 0. Two or more (fig. 130I). 1. One (fig. 131B).

287. PMS paracribellar spigots distribution: 0. On anterior margin of spinning field (figs. 107A, 130A, H). 1. Midfield (Griswold et al., 2005: figs. 73C, 77C). 2. At posterior margin of spinning field (fig. 130E). See Griswold et al. (2005: char. 91).

288. PMS paracribellar spigots encircling anteriorly: 0. Bunched (fig. 130H). 1. In a row, encircling anteriorly (fig. 130B). See Griswold et al. (2005: char. 92.) COMMENTS: *Filistata*: Pc posterior, inapplicable (scored -). *Neoramia*, *Stiphidion*: only two (scored -). *Metaltella*: dispersed (scored -). *Badumna*: midfield, inapplicable (scored -). *Pimus*: only one (scored -).

289. PMS paracribellar spigot base shape: 0. Cylindrical. 1. Long, narrow, flattened. See Griswold et al. (2005: char. 94.) State 1 is a synapomorphy of phyxelidids, not represented in this dataset.

290. PMS paracribellar spigot shaft: 0. Strobilate (fig. 130I). 1. Floppy (fig. 130E). The paracribellar spigots of filistatids are smooth, not strobilate, seemingly correlated with the smooth cribellar spigots (see char. 234).

291. PMS paracribellar spigot shafts grouping: 0. Every base with a single shaft. 1. Several shafts grouped on the same base. See Griswold et al. (2005: char. 93). Except for *Dictyna*, the fused paracribellars are monophyletic in this analysis (Clade 183). COMMENTS: *Metaltella*: some paracribellars with two shafts (scored 1).

292. PMS-PLS anterior claviform setae: 0. Absent. 1. Present (figs. 130D, F, G, 138B, E). This is a classic character of filistatids (Gray, 1995: char. 18; Ramírez and Grismado, 1997: char. 7), here found in prodidomines as well. COMMENTS: *Filistata*: one on PMS, contra Ramírez and Grismado (1997) (scored 1). *Prodidomus*: on PLS, flattened, look hyaline with stereoscope, but also on PMS in *Prodidomus dalmasi* (Platnick, 1990: fig. 131) (scored 1). *Neozimiris*: mostly on PLS, a few on PMS (scored 1).

293. PLS rows of claviform setae: 0. Absent. 1. Present. In *Prodidomus* and *Neozimiris*, the modified setae occur in one (fig. 138C) or more (fig. 138D) rows on the PLS.

294. Female PLS very short: 0. PLS long at least half the ALS. 1. Shorter than half ALS (fig. 113D). In this dataset only *Cryptothele* has extremely reduced PLS, with short basal segment, and distal segment just a crown of setae. The immature only bears short stubs, without spigots (fig. 113E).

295. PLS cylindrical gland spigots, number: 0. Six or more. 1. Five. 2. Four. 3. Three. 4. Two. 5. One. States are ordered. COMMENTS: *Raecius*: at least four (scored 012). *Petrichus*: right two, left three (scored 34). *Lauricius*: PLS partially collapsed (scored ?).

296. PLS modified spigot: 0. Absent. 1. Present (fig. 137D). For a discussion, see (Griswold et al., 2005: char. 96). COMMENTS: *Hypochilus*: see notes in Griswold et al. (2005: 30); in living specimens (thanks to Jason Bond, same as preparation MJR-863) I see consistently two spigots with thicker shafts, close together, paler (scored 1). *Stegodyphus*: interpreted according to Peters (1992) and Griswold et al. (2005) (scored 1). *Nicodamus*: apical nubbin on male PLS not symmetric (scored 0). *Macrobunus*: The cylindrical on female PLS is basal external, and might be confused with a modified PLS spigot. However, a subadult male has no large spigot on PLS (scored 0). *Homalonychus*: identified as modified PLS spigot because the male has a nubbin in that position (scored 1). *Oxyopes*: male with isolated apical group of longer spigots (scored 0). *Meriola*: small modified PLS spigot (scored 1). *Teutamus*: one aciniform only, distinguished from a modified PLS spigot because of the tartipore (scored 0). *Gnaphosa*: smaller than aciniforms, more visible in *G. sericata* and *G. parvula* (Platnick, 1990: fig. 7) (scored 1). *Legendrena*: identified as modified PLS spigot because it is larger than the only aciniform in female PMS (scored 1). *Vectius*: male without any spigot, female with a few small central nubbins (scored 0). *Trachycosmus*: no evident modified PLS spigot, but central spigot on male PLS with a sensilla associated (scored 0). *Syspira*: distinguishable only in male (scored 1). *Uliodon*: Imaged male with one large spigot on PLS, only on left side. Checked with more specimens: two other males lacking modified PLS spigot. The asymmetric scanned large spigot on preparation MJR-344 is interpreted as an anomaly (scored 0). *Ciniflella* BRA: only nubbins (scored ?). *Philodromus*: there is a nubbin on the male PLS, but also one on PMS, and the female does not have any larger spigot on PLS (scored 0). *Lyssomanes*: The apical larger spigots on PLS are accompanied by tartipores, hence they are not candidates for a modified PLS spigot. Scored as aciniform gland spigots in two size classes (scored 0).

297. PLS modified spigot conformation in adult male: 0. Nubbin (fig. 135B). 1. Spigot (fig. 136F). COMMENTS: *Eresus*: reduced (scored 01). *Stegodyphus*: from Griswold et al. (2005) (scored 1). *Psechrus*: from Griswold et al. (2005); note that the modified PLS spigot occurs in a male from Papua New Guinea (their figs. 100D, 102D), but is replaced by a nubbin in a male from Thailand (fig. 54D) (scored 1). *Meriola*: bad preparation (scored ?).

298. PLS modified spigot position: 0. Among the aciniforms, central (fig. 137C). 1. Marginal-apical (fig. 136E) or marginal-median (fig. 135E). 2. Marginal basal, segregated from the rest of the spigots (fig. 135D). COMMENTS: *Uloborus*, *Araneus*: marginal external median (scored 1). *Homalonychus*, *Galianoella*, *Legendrena*, *Neozimiris*: too few spigots to decide (scored 01). Trachelidae ARG: slightly marginal in female because of the very large cylindricals, central in male (scored 01).

299. PLS modified spigot accompanying spigots: 0. PLS modified spigot not particularly associated with other spigots (figs. 135G, 137B). 1. Closely associated with accompanying spigots (fig. 135A, F, H). COMMENTS: *Hypochilus*: some of the two or three spigots similar to modified PLS spigots could be accompanying spigots instead (scored 01). *Filistata*: The two paracribellars might be homologous to the ones in the triad of other cribellate spiders. Note the presence of paracribellar spigots in male (scored 01). *Titanoeca*: no modified PLS spigot (scored ?). *Homalonychus*: male only one nubbin (scored 0).

300. PLS modified spigot and accompanying spigot shafts on common base: 0. PLS modified spigot stands alone. 1. One shaft on same base as modified spigot (fig. 135J). This character is applicable only when accompanying spigots are present. It includes character 102 of Griswold et al. (2005), but has been extended to other accompanying spigot morphologies, not only paracribellars. COMMENTS: *Neoramia*: nubbins separate (scored 0). *Zorocrates*: present in the female, but nubbins well separated in the male (scored 01).

301. PLS spigots flanking the modified spigots, reduction in female: 0. Flanking spigots (fig. 135H). 1. Flanking nubbins (fig. 135I). COMMENTS: *Thaida*: one nubbin, one paracribellar spigot (scored 01). *Zorocrates*: right side with nubbin, left side with spigot (scored 01).

302. Kind of spigots accompanying the PLS modified spigots: 0. Paracribellars (fig. 135A). 1. Similar to aciniforms (fig. 135C). 2. Aggregates (fig. 135F). COMMENTS: *Thaida*: one paracribellar and a nubbin (scored 0). *Megadictyna*, *Dictyna*: one paracribellar (scored 0).

303. Anal tubercle size: 0. Small. 1. Very large (Griswold et al., 2005: fig. 27A). Oecobiids have a large anal tubercle fringed with setae. COMMENTS: *Austrachelas*: there are two distinct holes anterior to the anal tubercle (scored 0).

MALE PALP

The articles of the male palp are similar to those of the female and immatures in conformation and condyles, except that the male palp lacks a pretarsus and a claw, and has a copulatory bulb attached to the tarsus, an undisputed synapomorphy of spiders (figs. 139A, C, 140B). Males may have further secondary sexual structures on their palps, such as sclerotized processes or grooves. The brief list of secondary sexual structures presented here summarizes the most frequently found modifications in this dataset, and is only a fraction of the diversity found in spiders.

MALE PALPAL FEMUR MODIFICATIONS: The ventral side of the femur may have one or more processes, of which the most frequently found are the ventral basal (fig. 140H), the ventral median (fig. 140I), and the ventral apical (fig. 140E) processes.

MALE PALPAL PATELLA MODIFICATIONS: The retrolateral side of the patella may have a process (fig. 140G).

MALE PALPAL TIBIA MODIFICATIONS: A large clade of spiders have a retrolateral process (retrolateral tibial apophysis, RTA) on the tibia (fig. 140B), hence its name, the RTA clade. There may be other processes in addition to the RTA, such as the dorsal basal (fig. 140A), and the ventral apical (fig. 140D).

MALE PALPAL CYMBIUM AND ITS MODIFICATIONS: The tarsus of the male palp is modified to accommodate the copulatory bulb, and is called the *cymbium*. In entelegyne spiders the cymbium has a central depression, the alveolus, accommodating the spirally folded basal hematodocha (fig. 140F). The cymbium may have grooves, usually interacting with the embolus during copulation or in resting positions. Examples of such grooves are the apical cymbial groove (fig. 140F) ("cymbial conductor" of anyphaenids, Ramírez, 2003), and the retrolateral cymbial groove found in some miturgids (fig. 140B). Among the processes that usually occur on the cymbium, the most frequently found are two on the retrolateral margin of the alveolus: the retrobasal process, called the *paracymbium*, and the retromedial process; both processes can occur at the same time (fig. 140C). The dorsal surface of the cymbium has many chemosensory setae, which were found to be very sensitive to the pheromones released by females with their draglines (Tietjen and Rovner, 1980). The chemosensory setae may form a well-defined patch (fig. 140C).

COPULATORY BULB: The copulatory bulb has one or more sclerotized pieces called *sclerites*, and an internal blind duct, the spermophore (fig. 139A–C), discharging at the tip of the intromittent structure, the embolus. The copulatory bulb is not connected to the testis, hence the male must charge his bulbs by absorbing a drop of sperm through the embolus. The copulatory bulb is attached to the tarsus by a movable membrane, the basal hematodocha (fig. 140F). In primitive spiders the movements of the bulb are controlled by a pair of muscles, but in entelegynes the movement is entirely hydraulic, with the

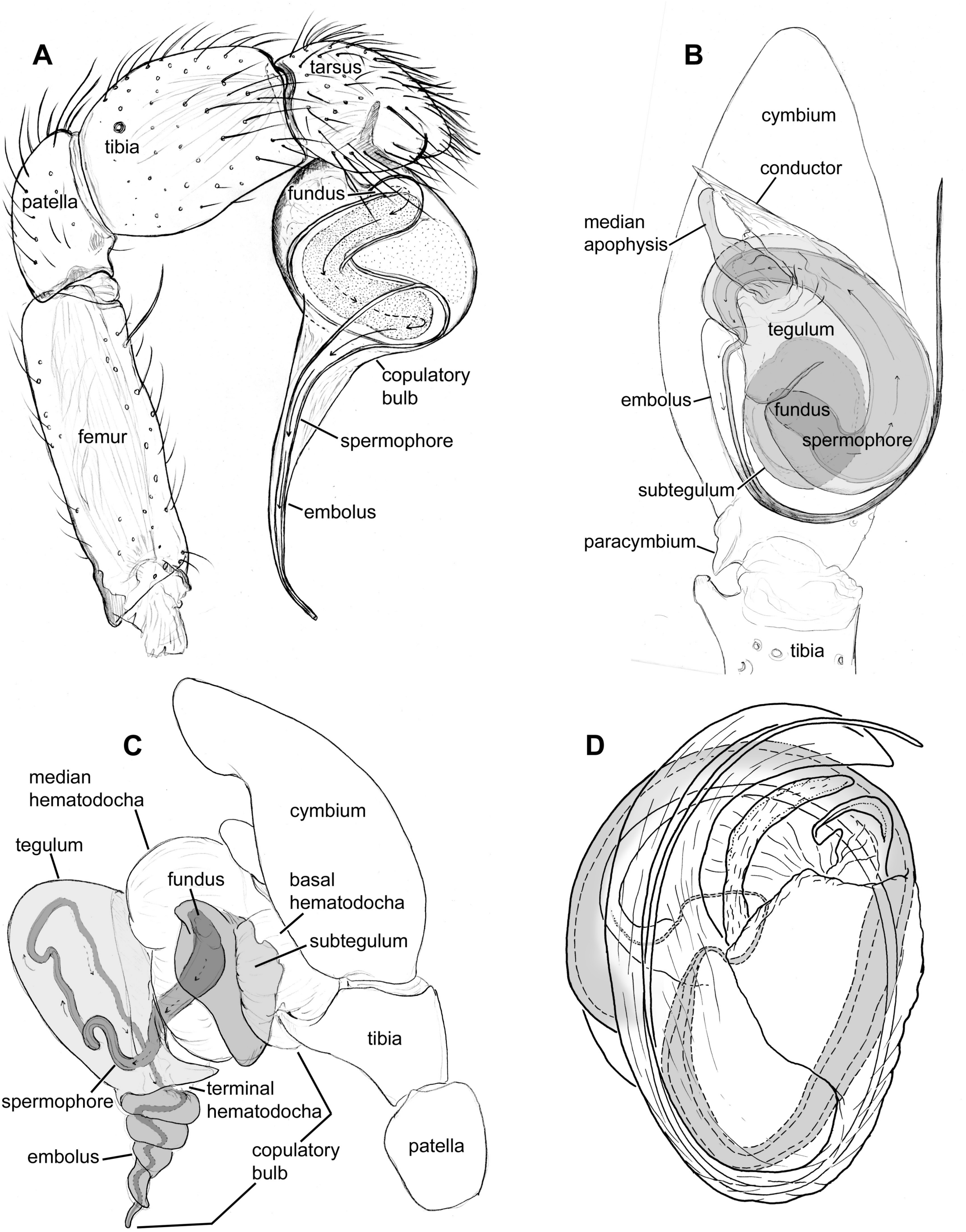

A
tarsus
tibia
patella
fundus
copulatory
bulb
femur
spermophore
embolus
B
cymbium
conductor
median
apophysis
tegulum
embolus
fundus
spermophore
subtegulum
paracymbium
tibia
C
median
hematodocha
cymbium
tegulum
fundus
basal
hematodocha
subtegulum
tibia
spermophore
terminal
hematodocha
embolus
copulatory
bulb
patella
D

Fig. 139. Structures of male palps, cleared. **A.** *Ariadna boesenbergi* (Segestriidae) left. **B.** Eutichuridae MAD (Eutichuridae) right. **C.** *Trachelas mexicanus* (Trachelidae) left. **D.** *Desis formidabilis* (Desidae) left bulb.

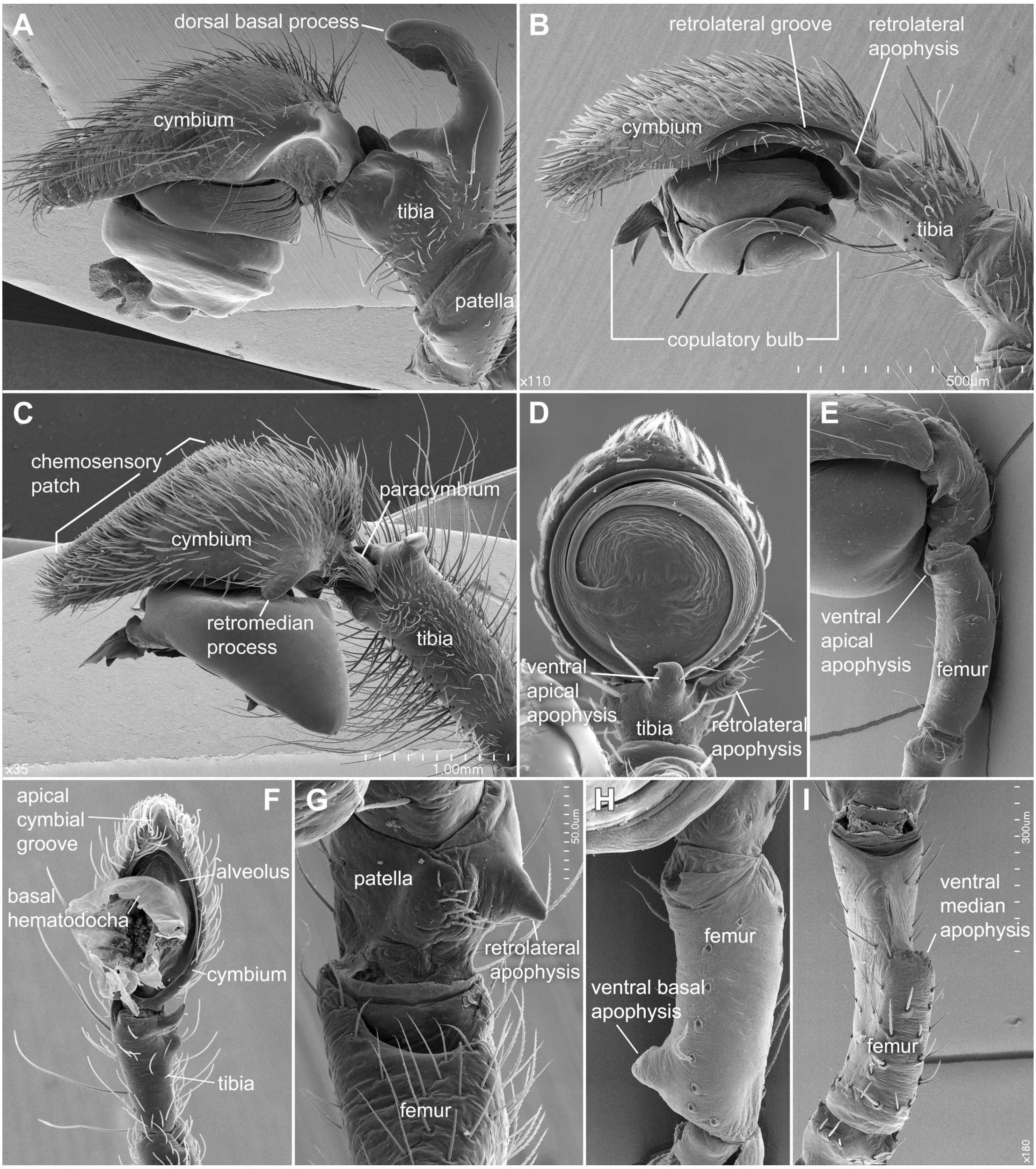

A
dorsal basal process
cymbium
tibia
patella
B
retrolateral groove
retrolateral apophysis
cymbium
tibia
copulatory bulb
x110
500um
C
chemosensory patch
cymbium
paracymbium
retromedian process
tibia
x35
1.00mm
D
ventral apical apophysis
tibia
retrolateral apophysis
E
ventral apical apophysis
femur
F
apical cymbial groove
alveolus
basal hematodocha
cymbium
tibia
G
patella
retrolateral apophysis
femur
50.0um
H
femur
ventral basal apophysis
I
ventral median apophysis
femur
300um
x180

Fig. 140. Structures of left male palps. **A.** *Nicodamus mainae* (Nicodamidae) retrolateral. **B.** *Zora spinimana* (Miturgidae) retrolateral. **C.** *Uliodon* cf. *frenatus* (Zoropsidae) retrolateral. **D.** *Boliscus* cf. *tuberculatus* (Thomisidae) ventral. **E.** *Orthobula calceata* (Phrurolithidae) retrolateral. **F.** *Xiruana gracilipes* (Anyphaenidae) ventral. **G.** *Trachelas minor* (Trachelidae) ventral. **H.** *Conifaber guarani* (Uloboridae) ventral-retrolateral. **I.** *Drassinella gertschi* (Phrurolithidae) ventral.

basal hematodocha greatly developed, and producing a significant rotation of the bulb as it inflates (Huber, 2004). In most spiders the copulatory bulb is formed by several sclerites articulated to each other via flexible or inflatable hematodochae (fig. 139C), but the sclerites may be fused in many different ways. For example, in many Haplogynae all the

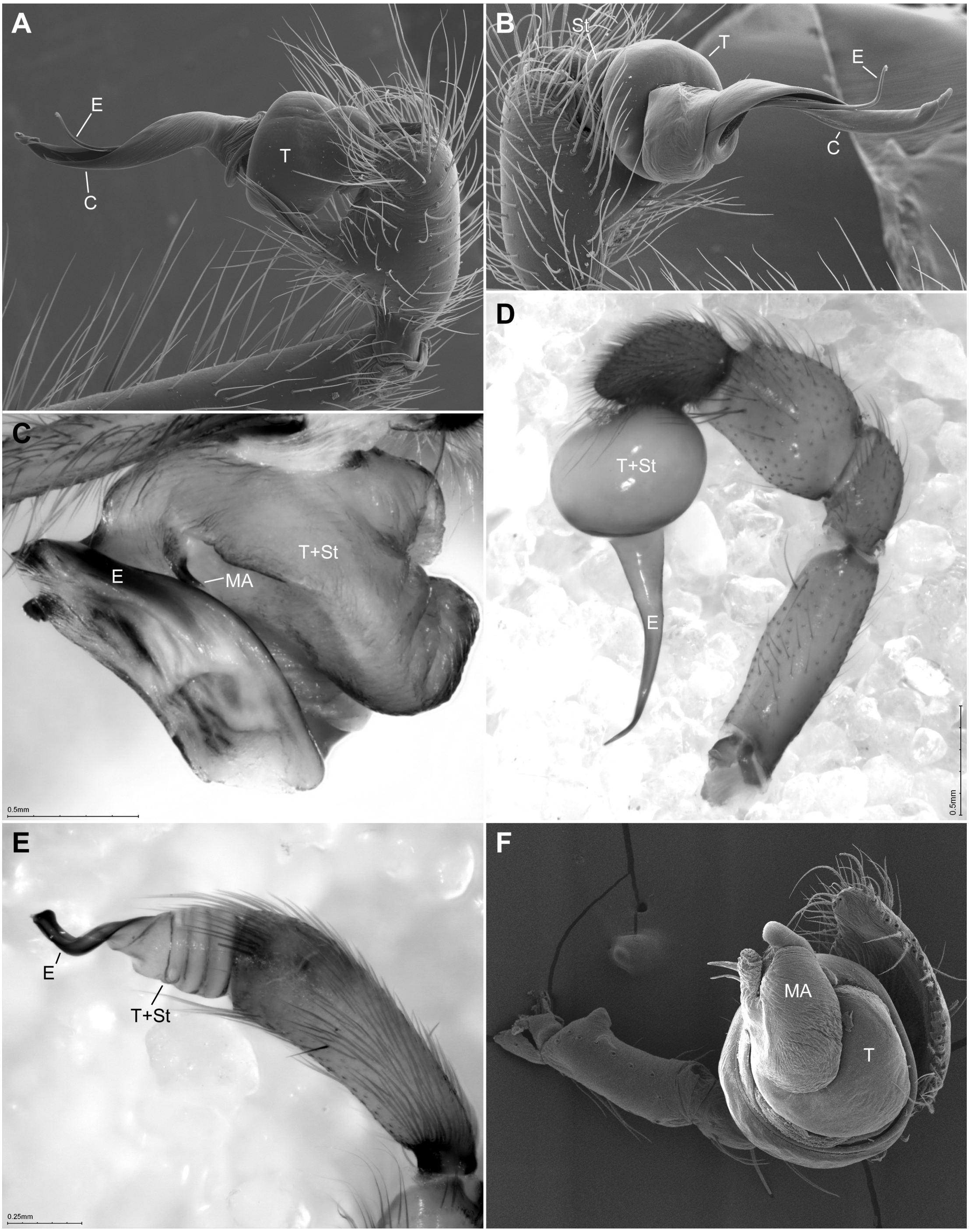

A
E
T
C
B
St
T
E
C
C
E
MA
T+St
0.5mm
D
T+St
E
0.5mm
E
E
T+St
0.25mm
F
MA
T

Fig. 141. Structures of male palps. **A.** *Hypochilus pococki* (Hypochilidae) left, retrolateral. **B.** Same, prolateral. **C.** *Thaida peculiaris* (Austrochilidae) left bulb, retrolateral. **D.** *Ariadna boesenbergi* (Segestriidae) right prolateral. **E.** *Kukulcania hibernalis* (Filistatidae) left retrolateral. **F.** *Conifaber guarani* (Uloboridae) left ventral.

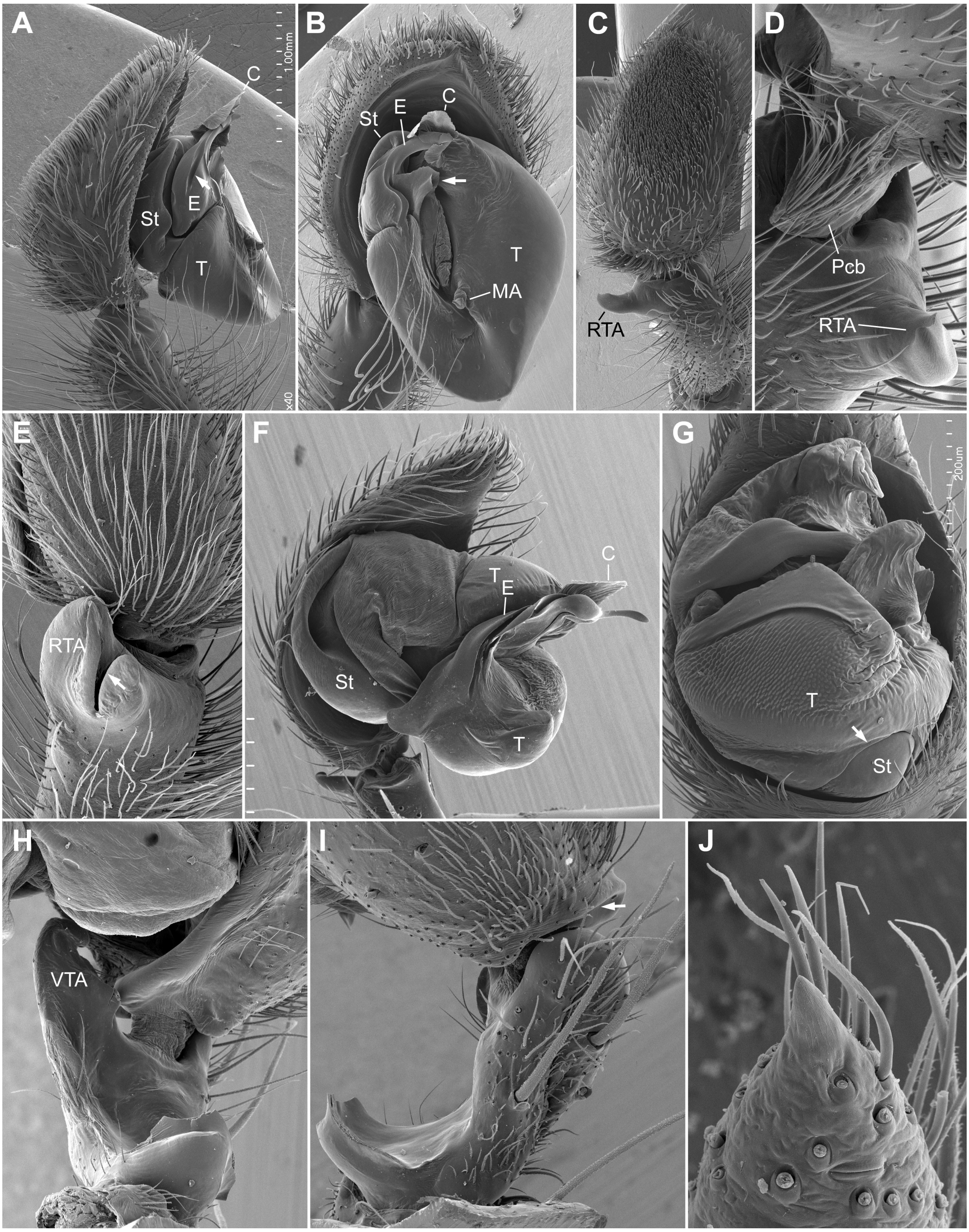


Fig. 142. Structures of left male palps. **A.** *Uliodon* cf. *frenatus* (Zoropsidae) prolateral, arrow to prolateral furrow on embolus. **B.** Same, ventral, arrow to hyaline flap at base of embolus. **C.** Same, dorsal. **D.** Same, retrolateral, articulation tibia-cymbium. **E.** *Desis formidabilis* (Desidae) retrolateral, articulation tibia-cymbium, arrow to canal on RTA. **F.** *Toxopsiella minuta* (Cycloctenidae) prolateral. **G.** *Pardosa moesta* (Lycosidae) ventral, arrow to regular indentation. **H.** *Oxyopes heterophthalmus* (Oxyopidae) tibia prolateral. **I.** Same, tibia and base of cymbium dorsal, arrow to transverse furrow on cymbium. **J.** *Senoculus* sp. (Senoculidae).

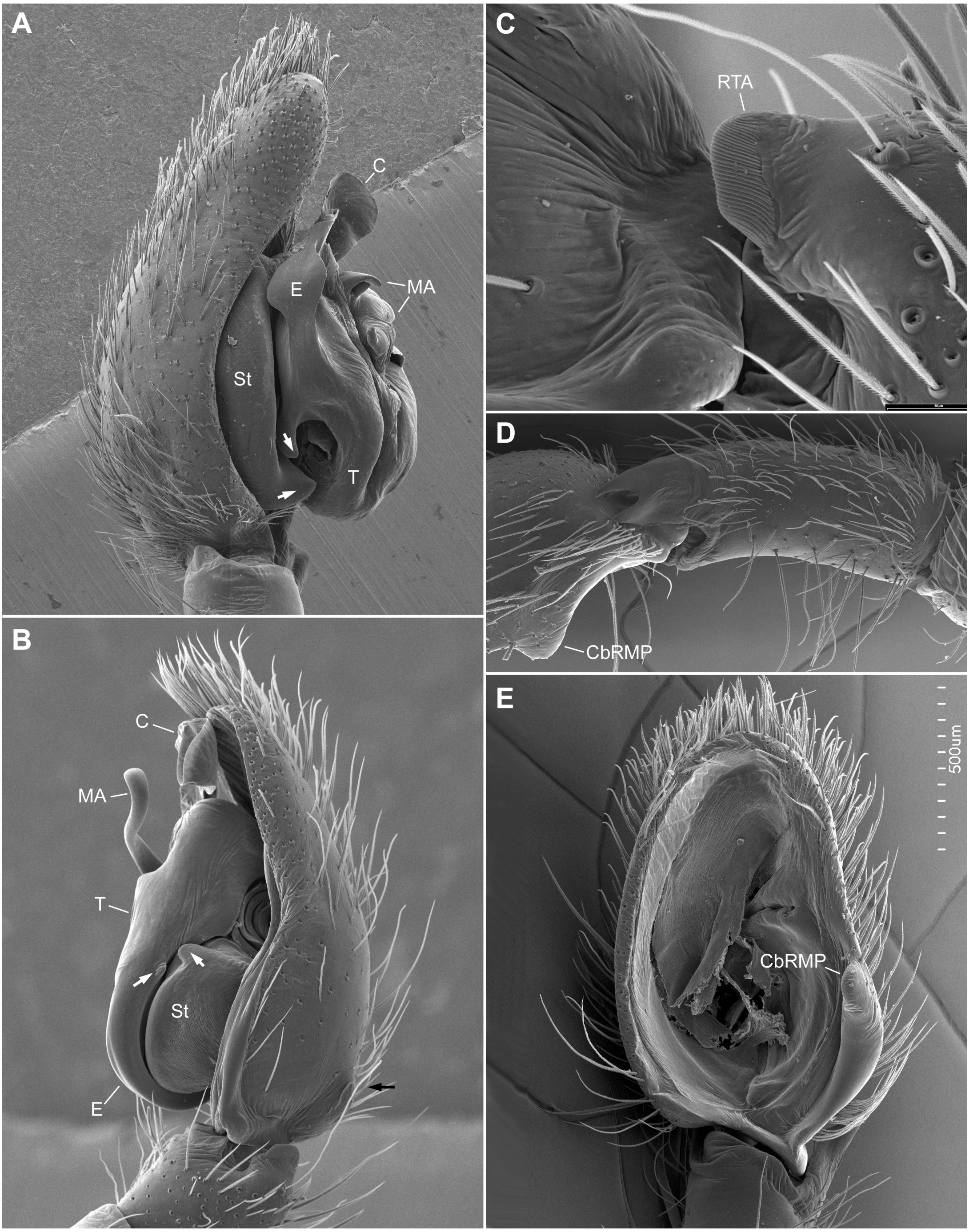


Fig. 143. Structures of left male palps. **A.** *Liocranoides unicolor* (Tengellidae) prolateral, arrows to tegular and subtegular locking lobes. **B.** *Ciniflella* ARG (Tengellidae) retrolateral; white arrows to tegular and subtegular locking lobes, black arrow to cymbial dorbasal projection. **C.** Same, articulation tibia-cymbium, showing file on RTA. **D.** *Lauricius hooki* (Tengellidae) tibia and cymbium retrolateral. **E.** Same, cymbium ventral.

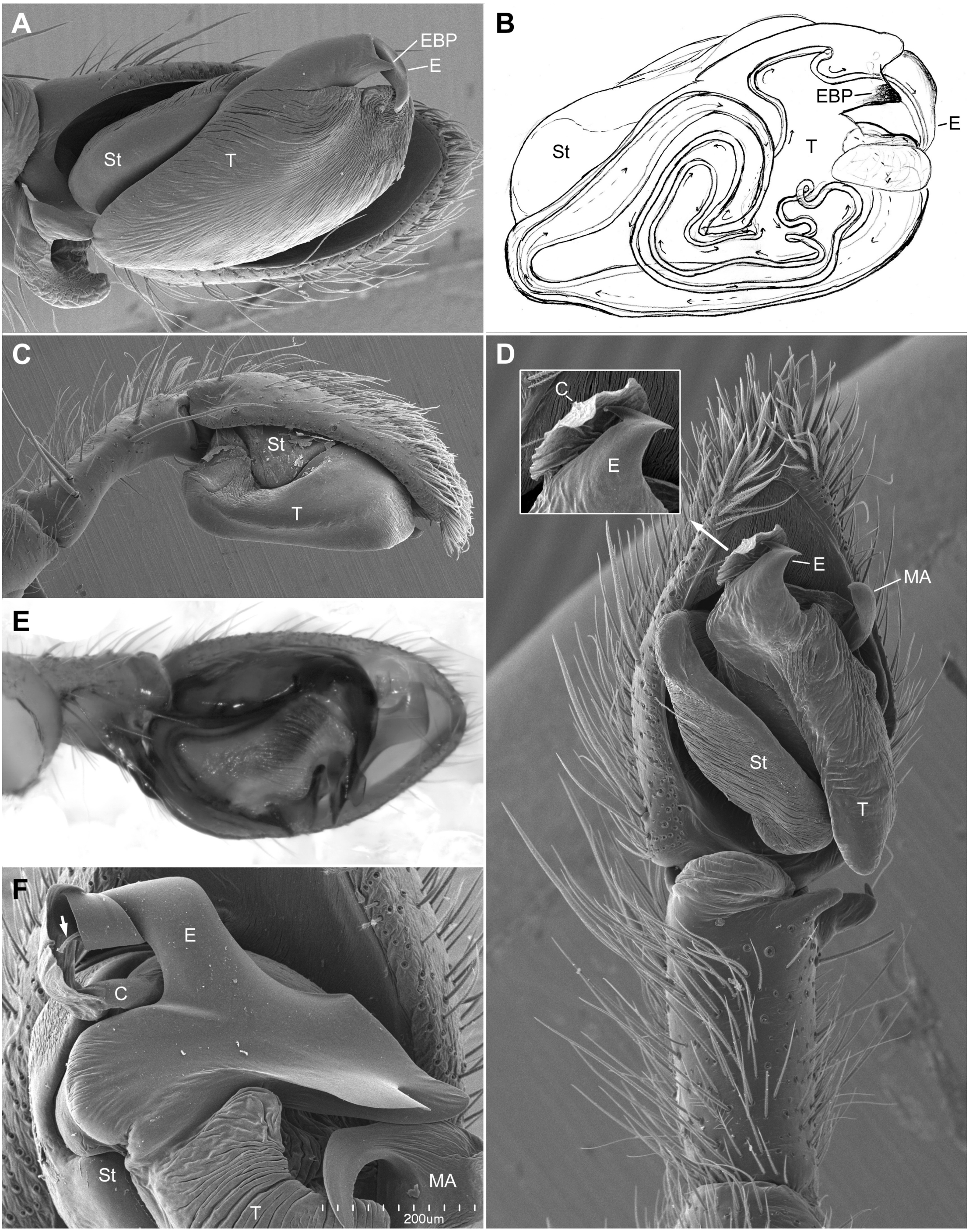

A
EBP
E
St
T
B
EBP
E
St
T
C
St
T
D
C
E
E
MA
St
T
E
F
E
C
St
MA
T
200um

Fig. 144. Structures of left male palps. **A.** *Clubiona pallidula* (Clubionidae) ventral. **B.** *Clubiona pallidula* (Clubionidae) bulb clarified, ventral. **C.** *Elaver* cf. *tigrinella* (Clubionidae) prolateral. **D.** *Neoanagraphis chamberlini* ("Liocranidae") ventral, inset with close-up of embolus. **E.** *Agroeca brunnea* ("Liocranidae") ventral. **F.** Same, detail of embolus, arrow to thin ending of embolus.

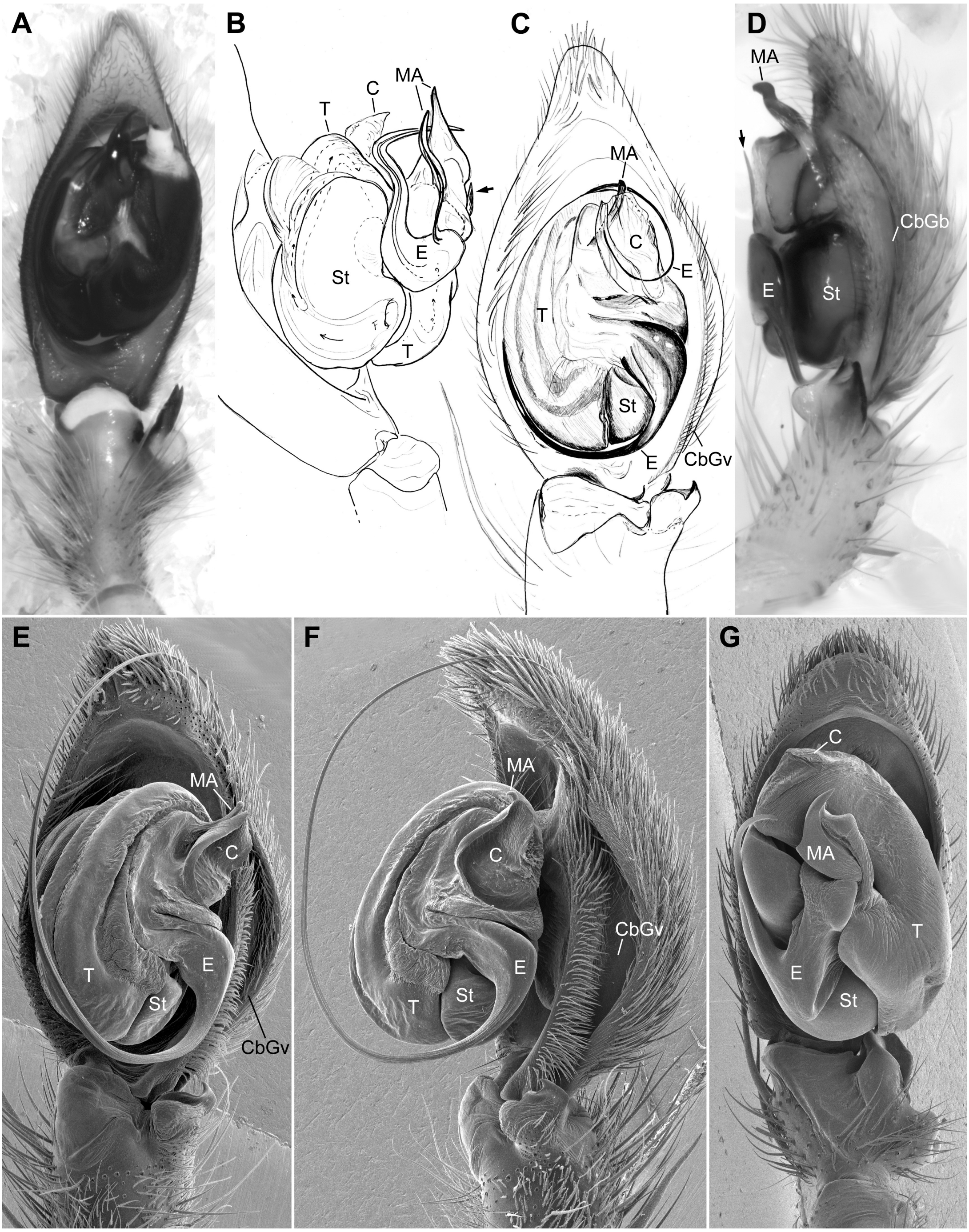

A
B
T
C
MA
E
St
T
C
MA
C
E
T
St
E
CbGv
D
MA
CbGb
E
St
E
MA
C
T
E
St
CbGv
F
MA
C
CbGv
E
T
St
G
C
MA
T
E
St

Fig. 145. Structures of left male palps of Miturgidae. **A.** *Miturga* cf. *lineata* ventral. **B.** Same, prolateral, bulb partially expanded, arrow to spine-shaped sclerite parallel to the median apophysis. **C.** *Syspira eclectica* ventral, arrow to pointed anterior projection of the median apophysis. **D.** *Elassoctenus* sp., retrolateral, arrow to spine-shaped sclerite parallel to the median apophysis. **E.** *Syspira eclectica* ventral. **F.** Same, retrolateral. **G.** Miturgidae QLD, ventral.

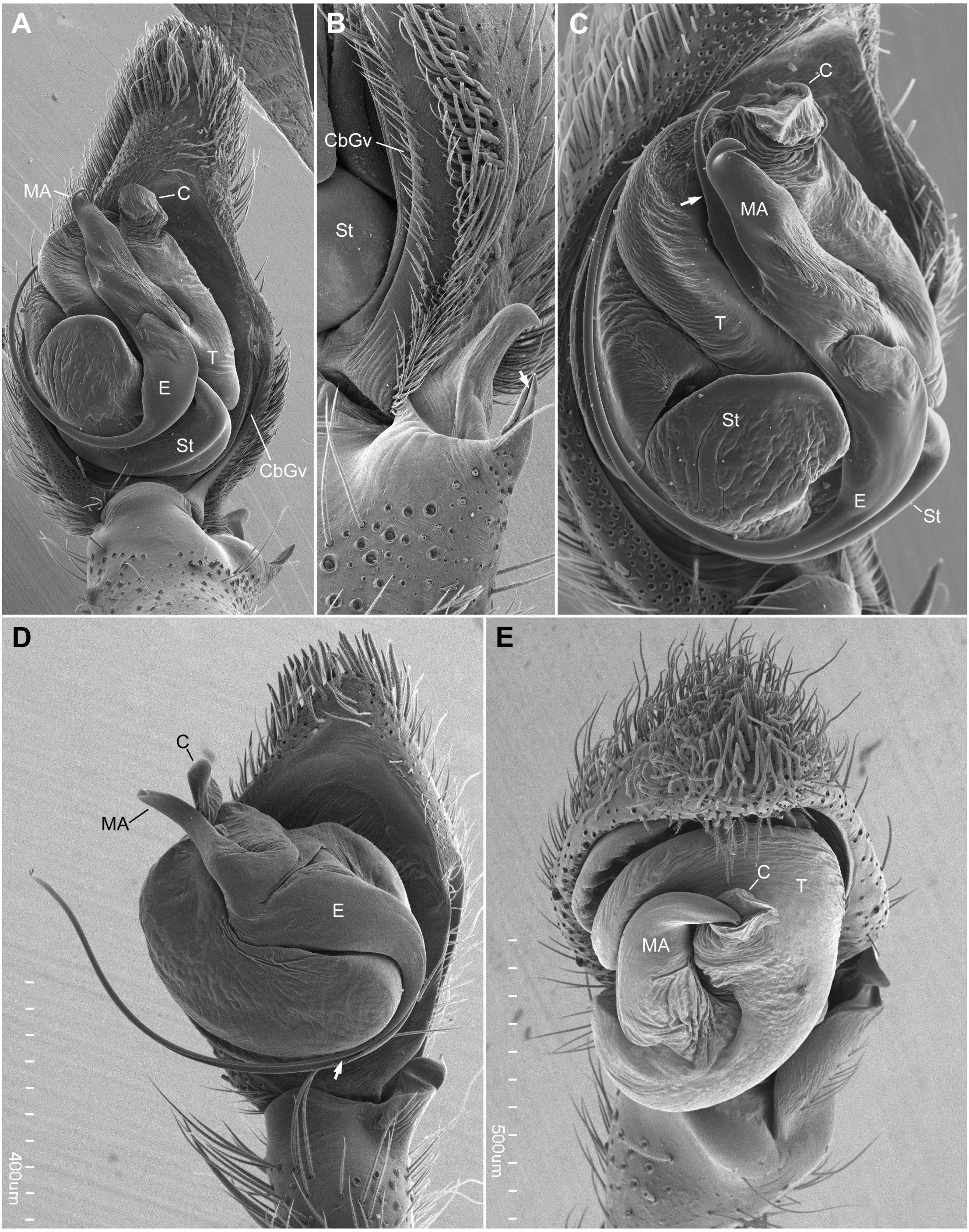

A
MA
C
T
E
St
CbGv
B
CbGv
St
C
C
MA
T
St
E
St
D
C
MA
E
400um
E
C
T
MA
500um

Fig. 146. Structures of male palps of Miturgidae, left. **A.** *Miturga gilva* ventral. **B.** Same, articulation tibia-cymbium, retrolateral, arrow to canal on RTA. **C.** Same, prolateral-ventral, arrow to pointed anterior projection of the median apophysis. **D.** *Zora spinimana* ventral, arrow to furrow on embolus. **E.** *Systaria* sp. ventral-apical.

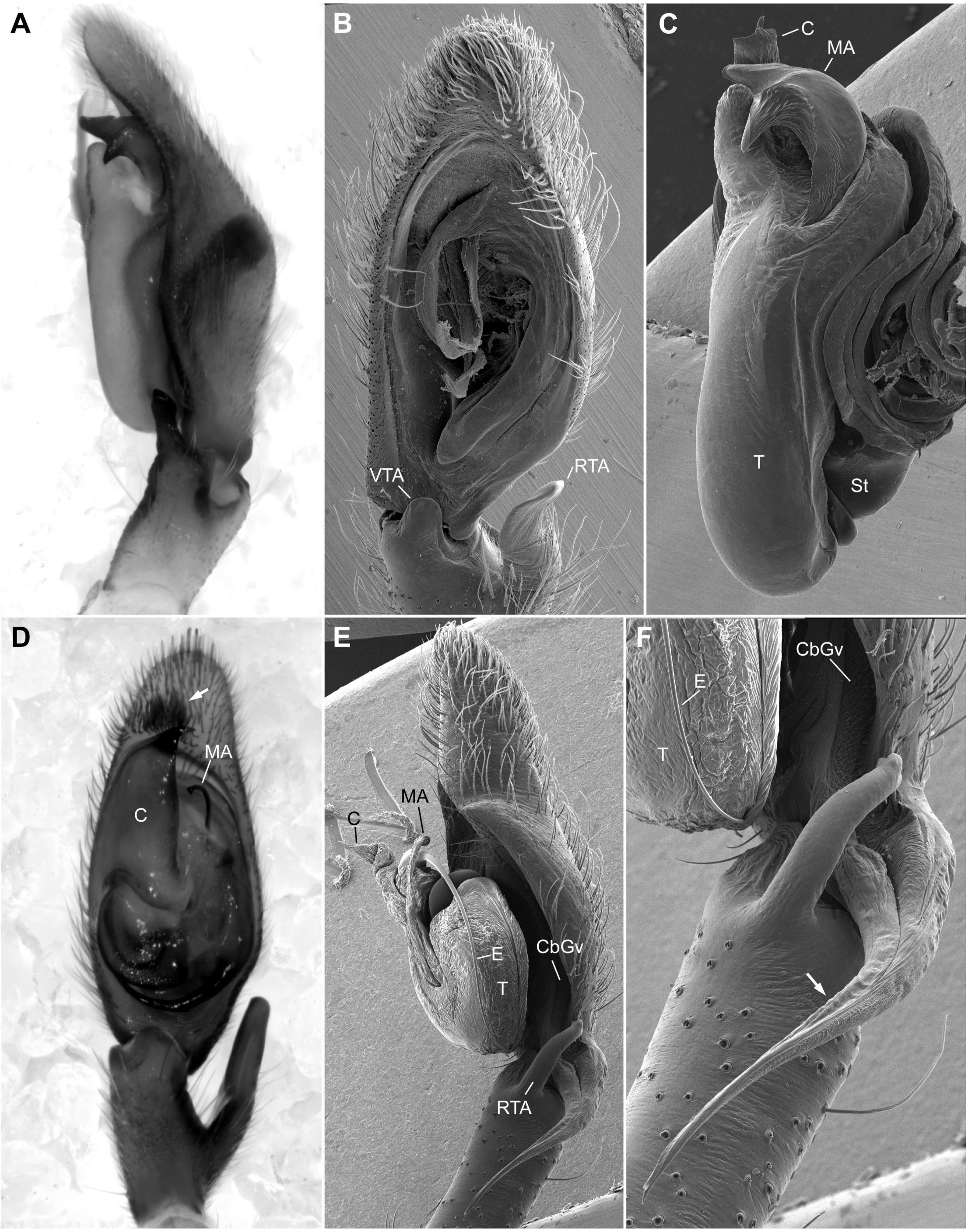

A
B
VTA
RTA
C
C
MA
T
St
D
MA
C
E
MA
C
E
CbGv
T
RTA
F
CbGv
E
T

Fig. 147. Structures of left male palps of Eutichuridae. **A.** *Eutichurus lizeri* retrolateral. **B.** Same, cymbium ventral. **C.** Same, copulatory bulb retrolateral. **D.** *Lessertina mutica* ventral, arrow to bunch of thick setae on cymbium. **E.** *Cheiracanthium punctorium* retrolateral. **F.** Same, articulation tibia-cymbium, arrow to posterior extension of cymbial groove.

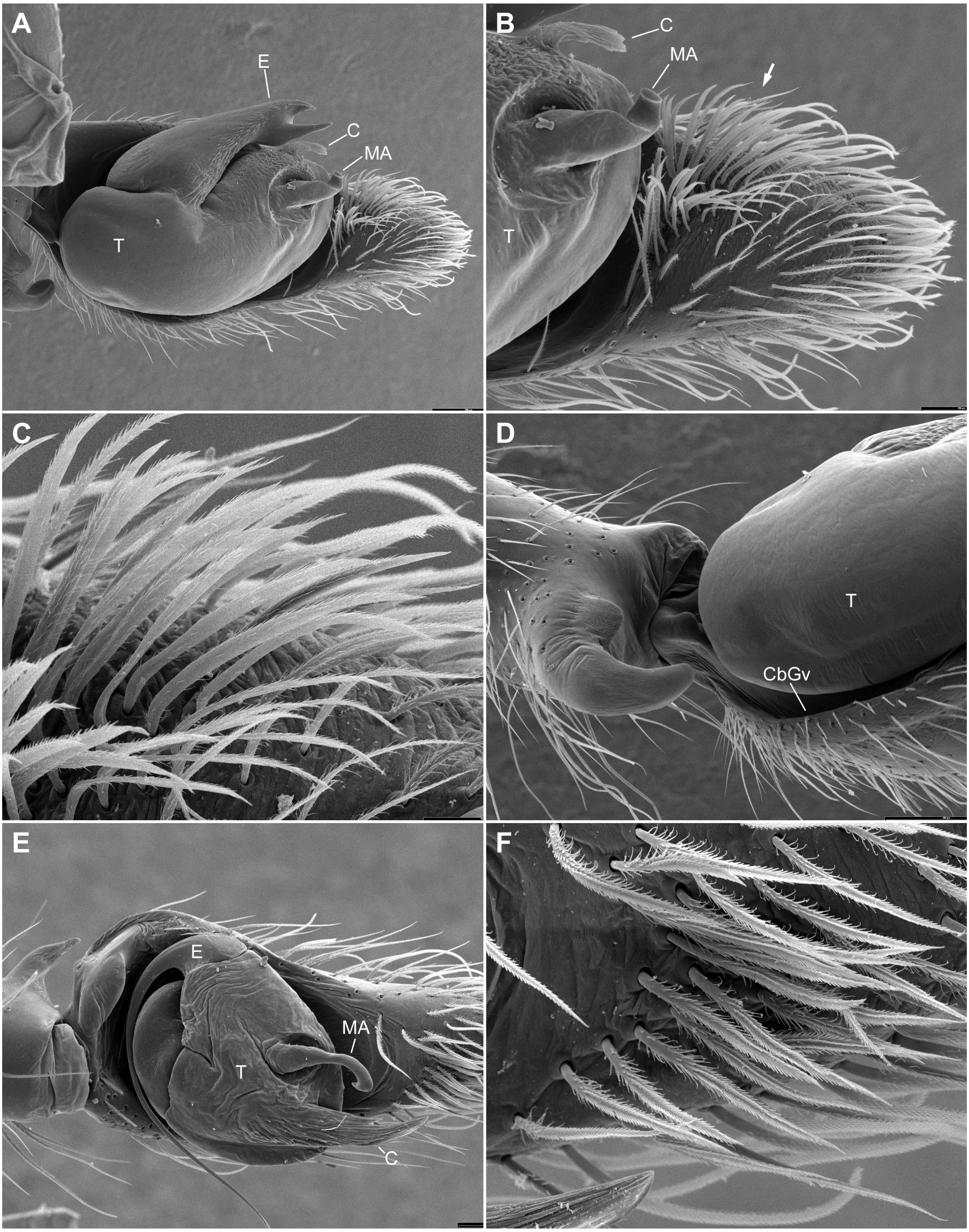


Fig. 148. Structures of male palps of Eutichuridae and potential relatives. **A.** *Cheiramiona* sp. ventral, left. **B.** Same, detail of apical portion, arrow to thick setae on cymbium. **C.** Same, detail of thick setae. **D.** Same, articulation tibia-cymbium, retrolateral. **E.** Cf. Eutichuridae QLD ventral, right. **F.** Same, detail of bunch of thick setae on cymbium.

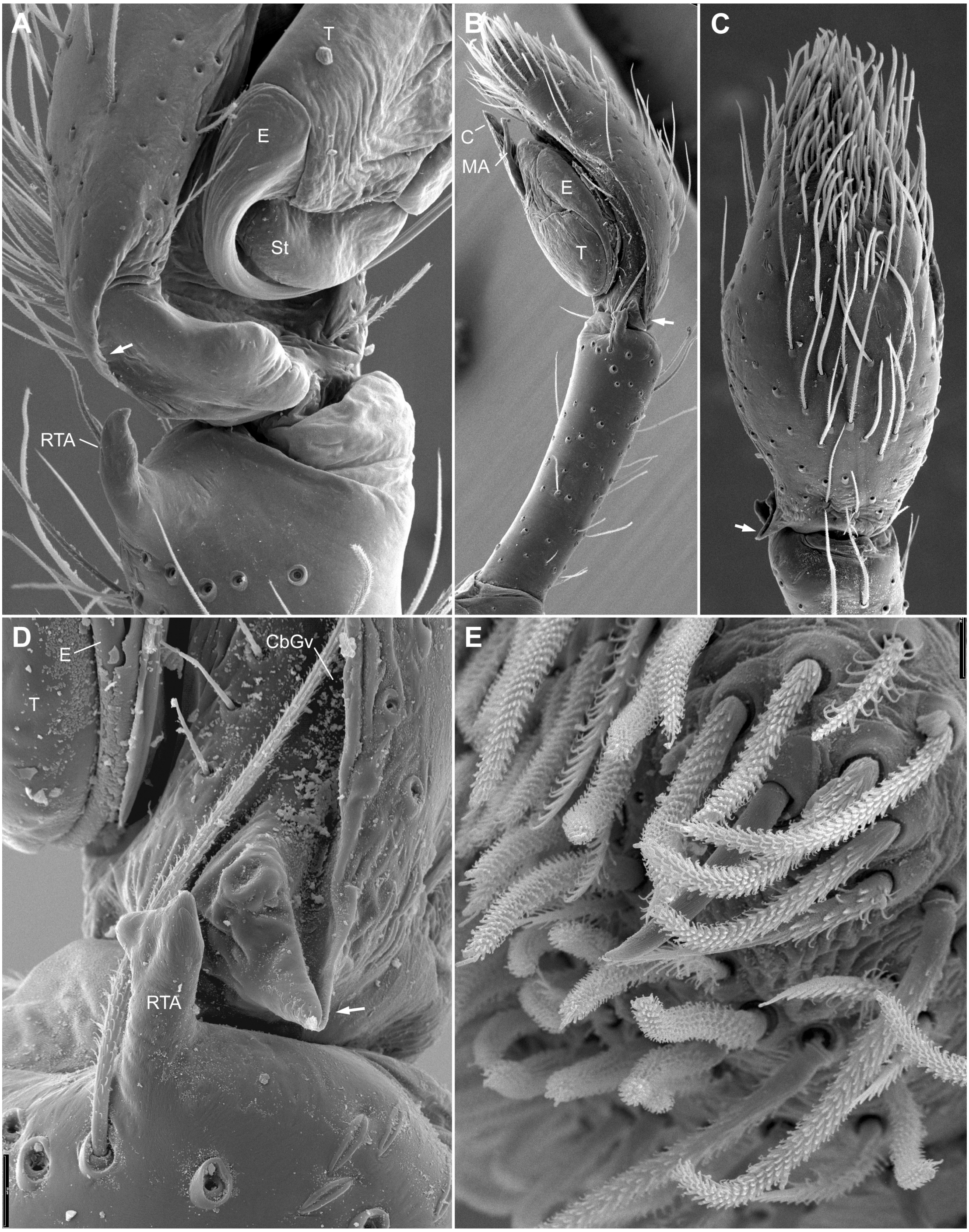


Fig. 149. Structures of male palps of Eutichuridae and potential relatives. **A.** Cf. Eutichuridae QLD, right articulation tibia-cymbium, retrolateral, arrow to superficial cymbial groove. **B.** Eutichuridae MAD, left, retrolateral, arrow to posterior extension of cymbial groove. **C.** Same, cymbium dorsal, arrow to to posterior extension of cymbial groove. **D.** Same, articulation tibia-cymbium, retrolateral, arrow to to posterior extension of cymbial groove. **E.** Same, tip of cymbium, apical.

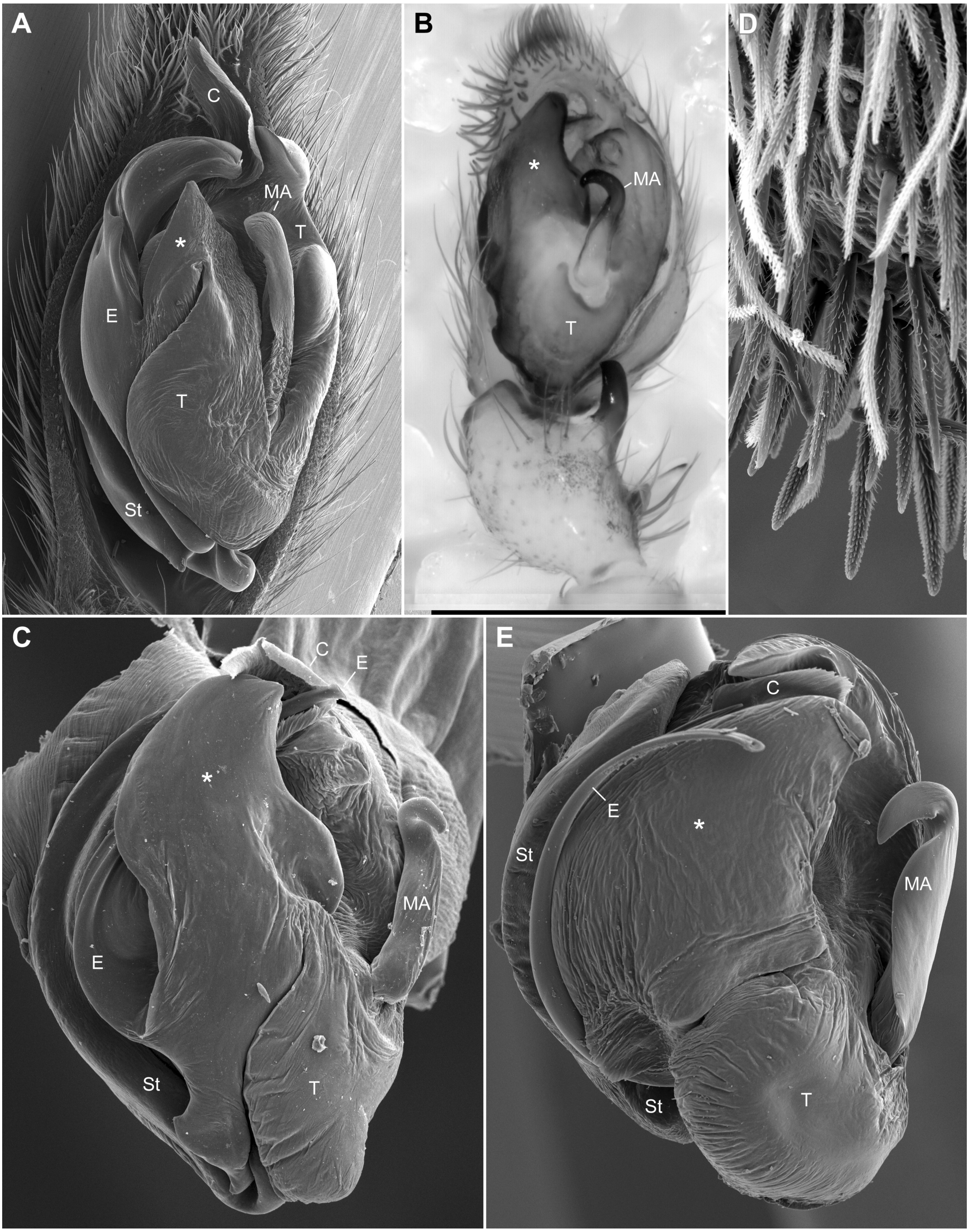

A
C
MA
T
*
E
T
St
B
*
MA
T
D
C
C
E
*
MA
E
St
T
E
C
E
St
*
MA
St
T

Fig. 150. Structures of left male palps of the *Xenoctenus* group. **A.** *Xenoctenus* sp., ventral. **B.** *Paravulsor* sp., ventral. **C.** Same, copulatory bulb ventral. **D.** *Odo bruchi*, thick setae near tip of cymbium. **E.** Same, copulatory bulb ventral. (Asterisks on tegular distal division at embolar base.)

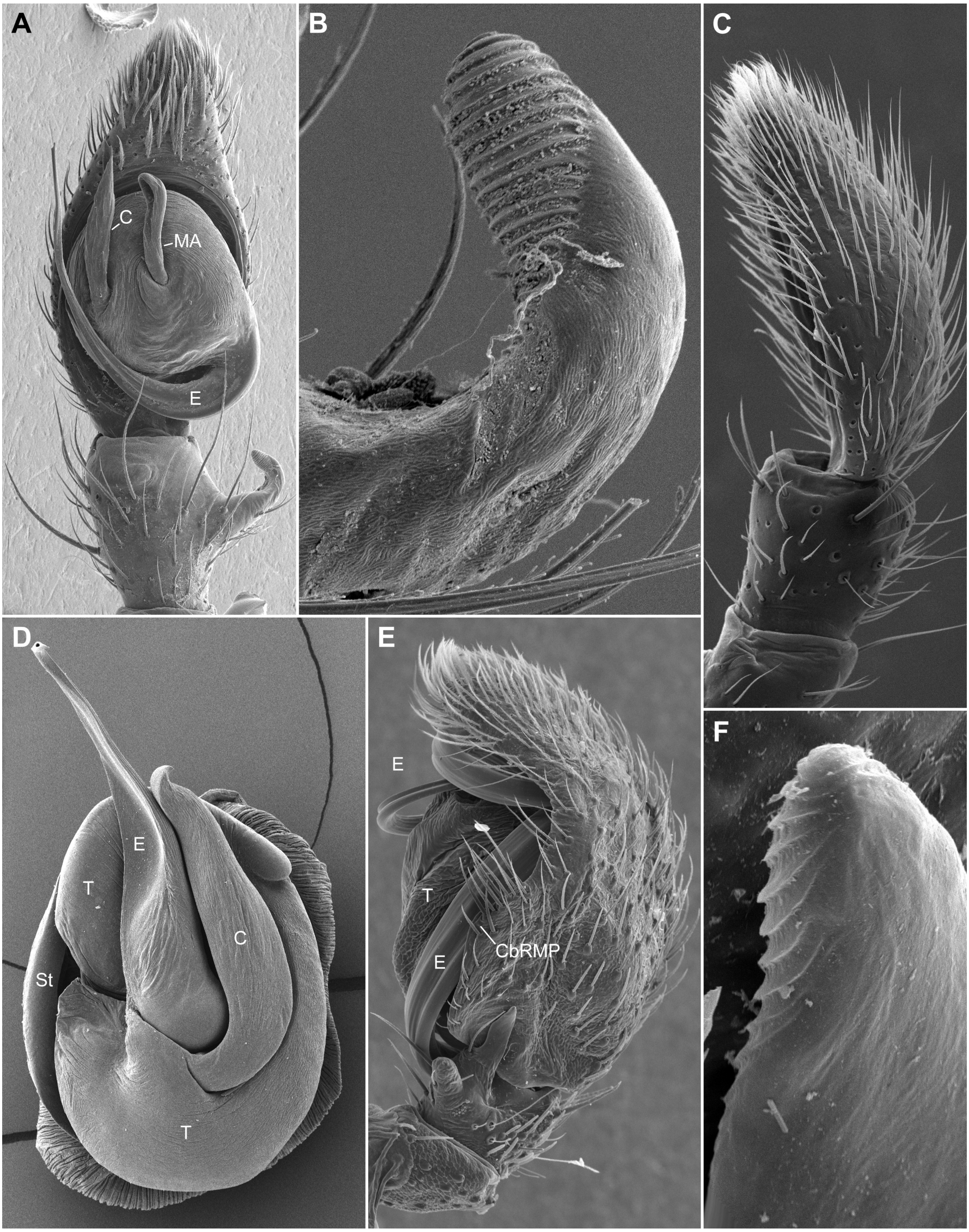


Fig. 151. Structures of left male palps of representatives of Thomisidae usually placed in "Stephanopinae." **A.** *Geraesta hirta* ventral. **B.** Same, detail of file on RTA. **C.** *Stephanopoides brasiliana*, tibia and cymbium retrolateral. **D.** *Cebrenninus rugosus*, copulatory bulb ventral. **E.** *Stephanopis ditissima* retrolateral. **F.** Same, detail of file on RTA.

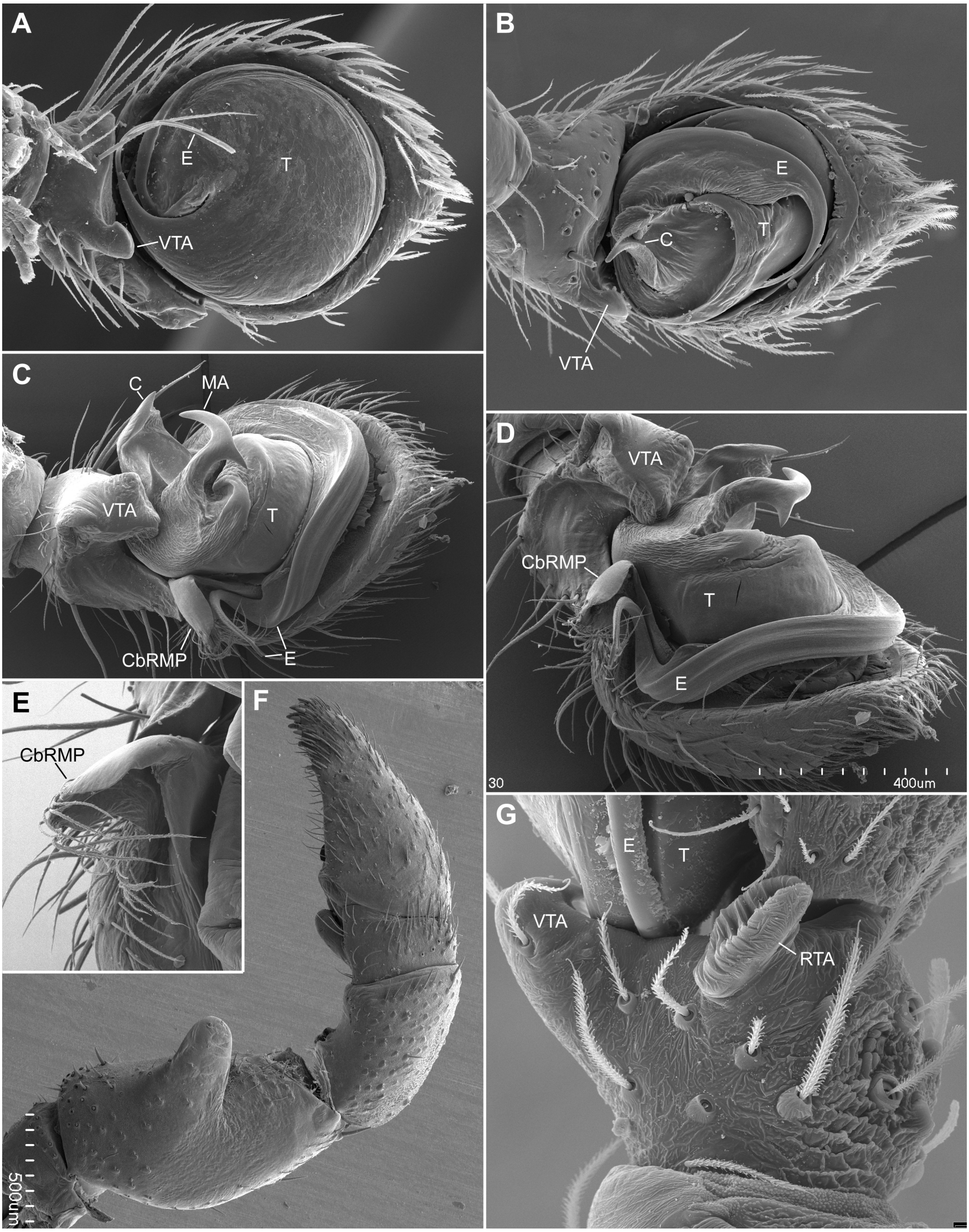

A
E
T
VTA
B
E
C
T
VTA
C
C
MA
VTA
T
CbRMP
E
D
VTA
CbRMP
T
E
30
400um
E
CbRMP
F
500um
G
E
T
VTA
RTA

Fig. 152. Structures of left male palps of higher Thomisidae. **A.** *Thomisus onustus* ventral. **B.** *Tmarus holmbergi* ventral. **C.** *Xysticus cristatus* ventral-apical. **D.** Same, apical, showing cymbial retromedian process (tutaculum). **E.** Same, detail of tutaculum. **F.** *Aphantochilus rogersi* retrolateral. **G.** *Boliscus* cf. *tuberculatus* tibia retrolateral.

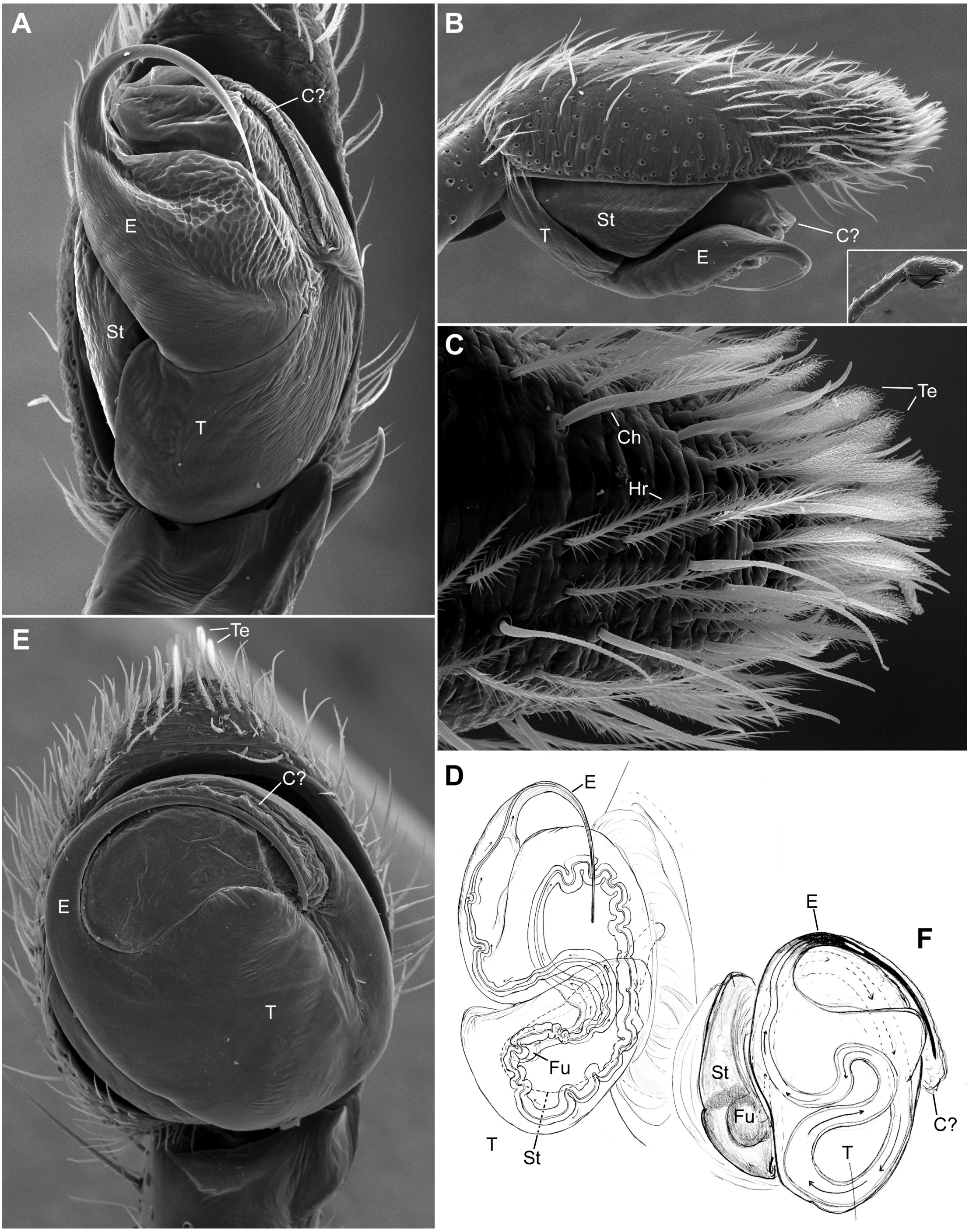

A
C?
E
St
T
B
St
T
C?
E
C
Te
Ch
Hr
E
Te
C?
E
T
D
E
Fu
T
St
E
F
St
Fu
C?
T

Fig. 153. Structures of left male palps of Philodromidae. **A.** *Titanebo mexicanus* ventral. **B.** Same, prolateral, inset showing whole tibia. **C.** Same, tip of cymbium, ventral, showing tenent setae. **D.** Same, copulatory bulb partially expanded. **E.** *Petrichus* sp. ventral. **F.** Same, copulatory bulb partially expanded.

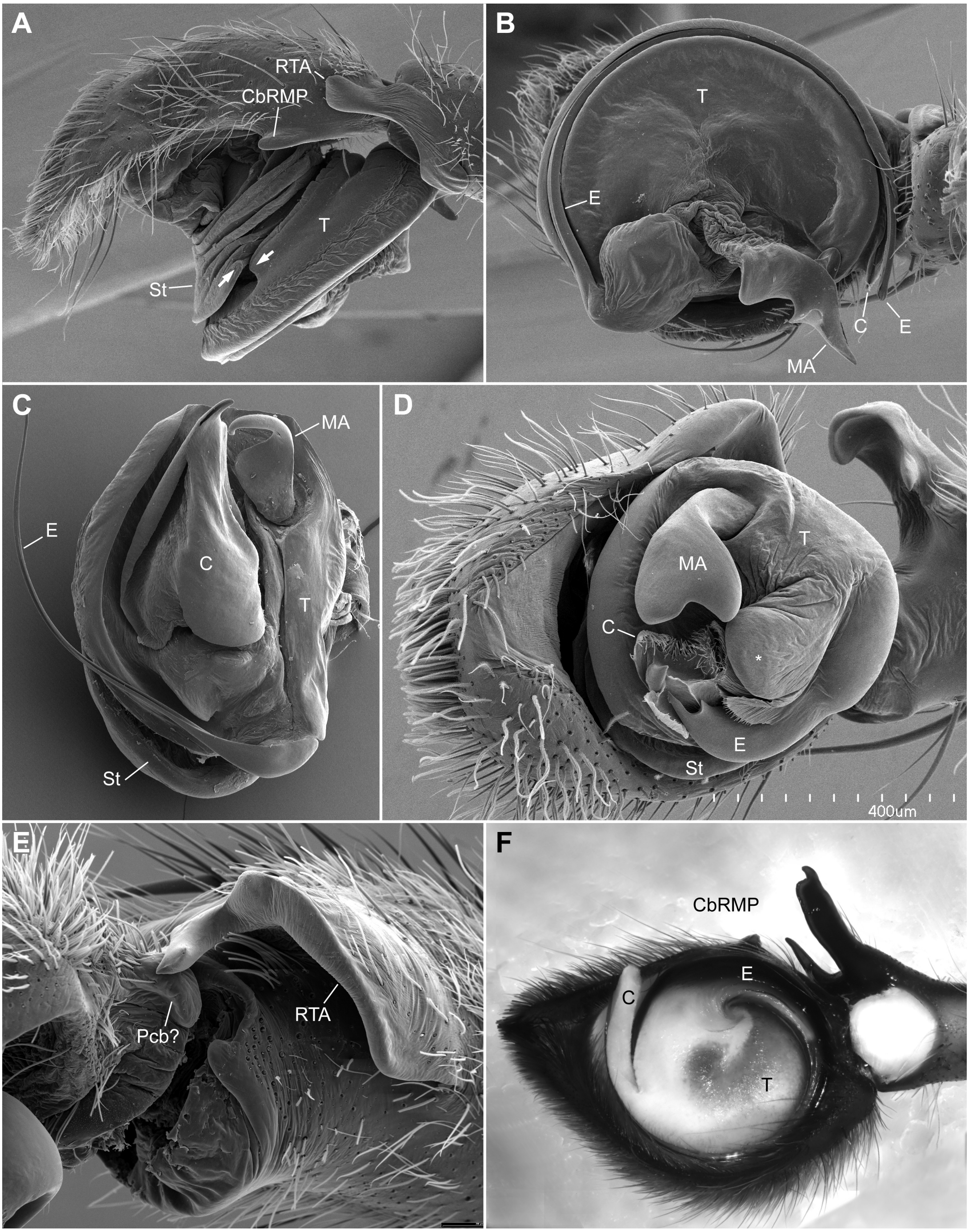

A
RTA
CbRMP
T
St
B
T
E
C
E
MA
C
MA
E
C
T
St
D
T
MA
C
*
E
St
400um
E
Pcb?
RTA
F
CbRMP
E
C
T

Fig. 154. Structures of left male palps of Selenopidae and Sparassidae. **A.** *Anyphops* sp. (Selenopidae) retrolateral, arrows to supplementary locking lobes on retrolateral side. **B.** Same, ventral. **C.** *Selenops debilis* (Selenopidae) copulatory bulb ventral. **D.** Sparianthinae VEN Trinidad (Sparassidae) apical-ventral, asterisk on sclerite near base of embolus. **E.** *Heteropoda venatoria* (Sparassidae) articulation tibia-cymbium, retrolateral. **F.** *Polybetes pythagoricus* (Sparassidae) ventral.

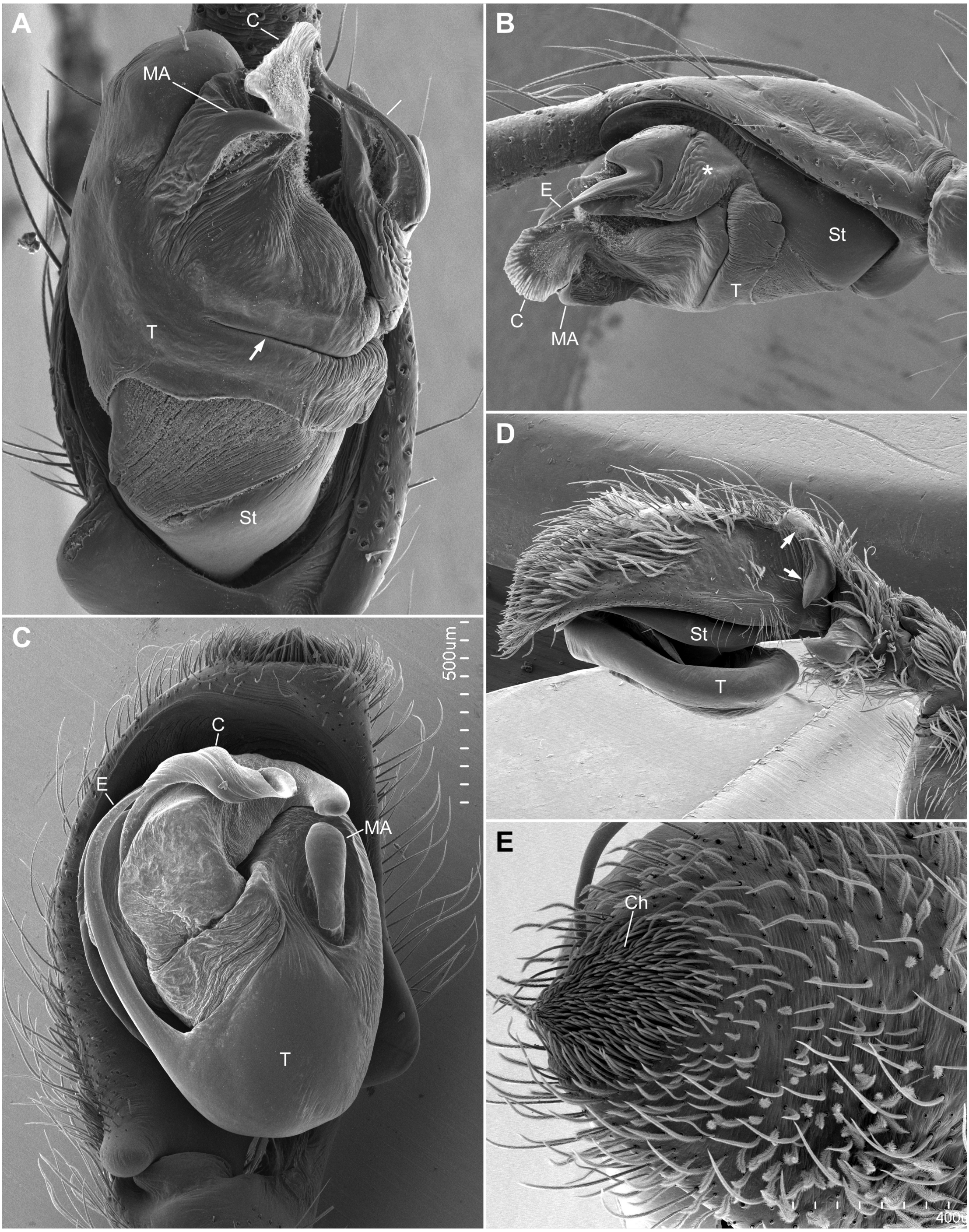

A
C
MA
T
St
B
E
*
St
C
MA
T
D
St
T
C
500um
C
E
MA
T
E
Ch
400

Fig. 155. Structures of male palps of Salticidae. **A.** *Lyssomanes viridis* ventral, arrow to transverse furrow on tegulum. **B.** Same, prolateral, asterisk on separate embolar division. **C.** *Holcolaetis* cf. *zuluensis* ventral. **D.** *Portia schultzi* retrolateral, arrows to cymbial dorsobasal projection. **E.** Same, tip of cymbium, dorsal-apical.

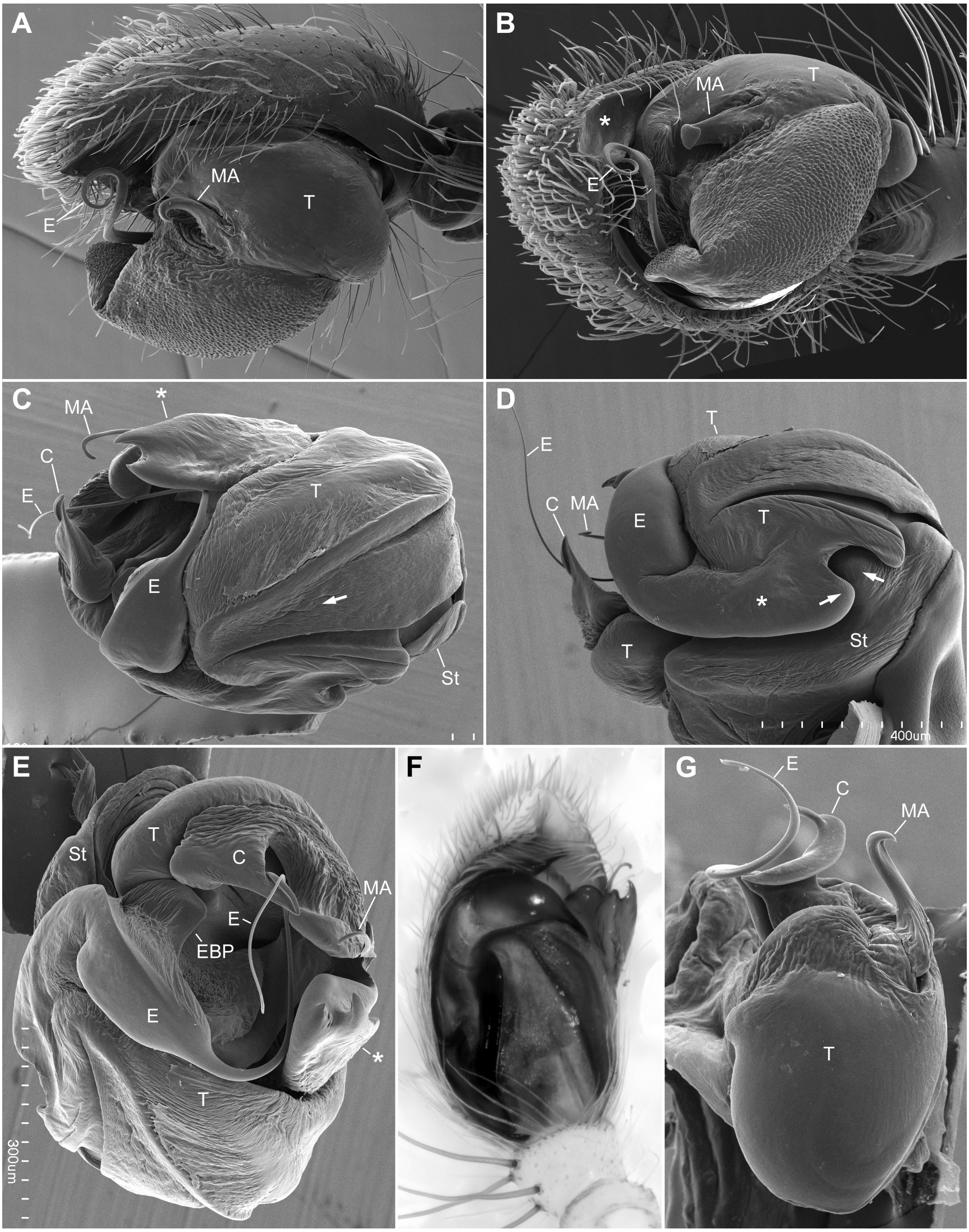

A
E
MA
T
B
MA
T
*
E
C
MA
*
C
E
T
E
St
D
T
E
C
MA
E
T
*
St
T
400um
E
St
T
C
MA
E
EBP
E
*
T
300um
F
G
E
C
MA
T

Fig. 156. Structures of left male palps of Anyphaenidae. **A.** *Anyphaena accentuata* retrolateral. **B.** Same, ventral, asterisk on cymbial apical groove. **C.** *Gayenna americana* ventral; asterisk to paramedian apophysis, arrow to regular notch. **D.** Same, prolateral; asterisk to partially separate embolic division, arrows to tegular (embolar base) and subtegular locking lobes. **E.** Same, apical, asterisk to paramedian apophysis. **F.** Same, ventral. **G.** *Xiruana gracilipes* ventral.

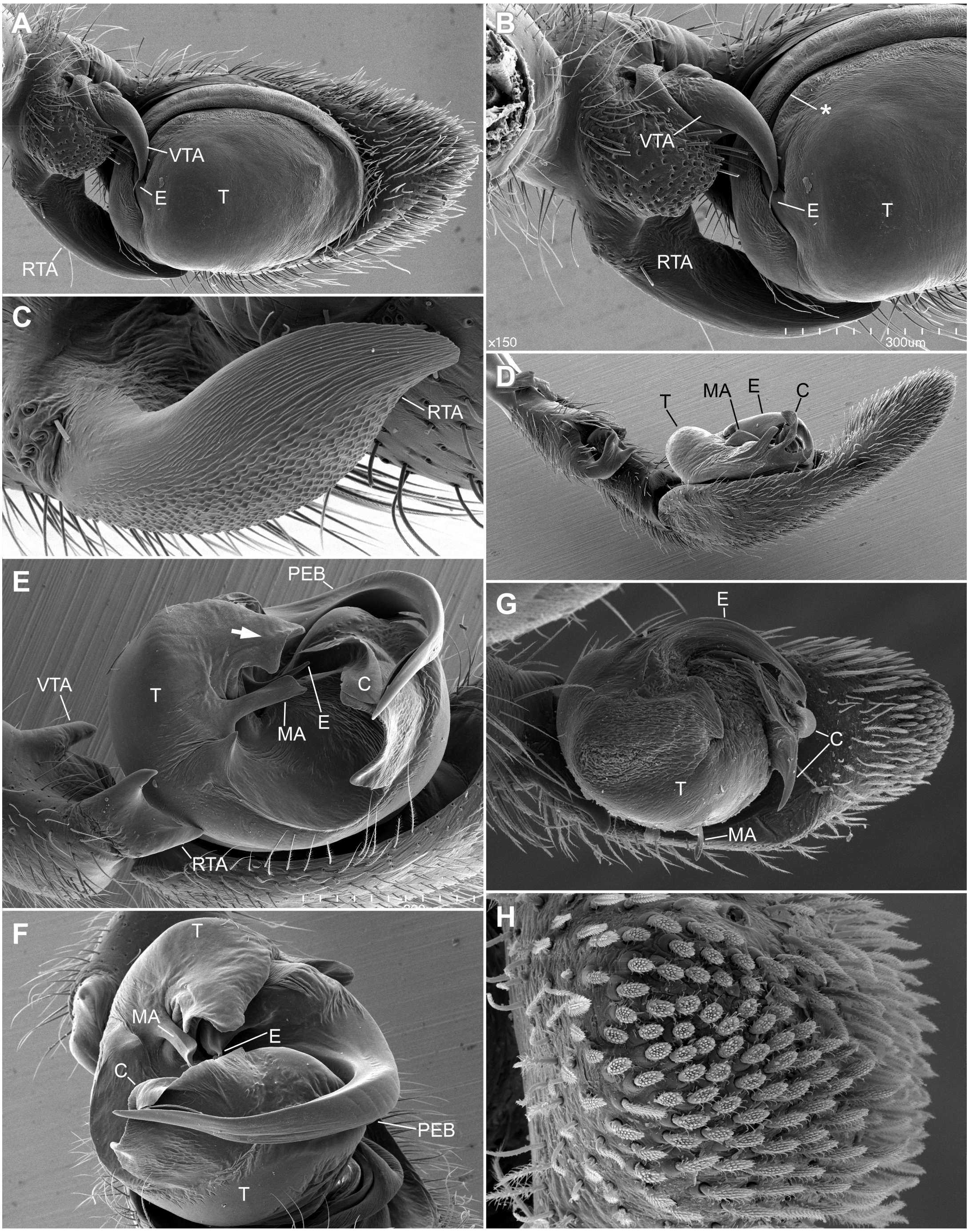

A
VTA
E
T
RTA
B
*
VTA
E
T
RTA
x150
300um
C
RTA
D
T
MA
E
C
E
PEB
VTA
T
C
MA
E
RTA
F
T
MA
E
C
PEB
T
G
E
C
T
MA
H

Fig. 157. Structures of left male palps of "basal corinnids." **A.** *Brachyphaea* cf. *simoni* ventral. **B.** Same, tibia and part of bulb, asterisk to tegular furrow holding embolus. **C.** Same, RTA, retrolateral. **D.** *Procopius* cf. *aetiops* retrolateral. **E.** *Pseudocorinna felix* retrolateral, arrow to additional sclerite near embolus. **F.** Same, apical. **G.** *Pronophaea proxima* ventral. **H.** Same, tip of cymbium, apical.

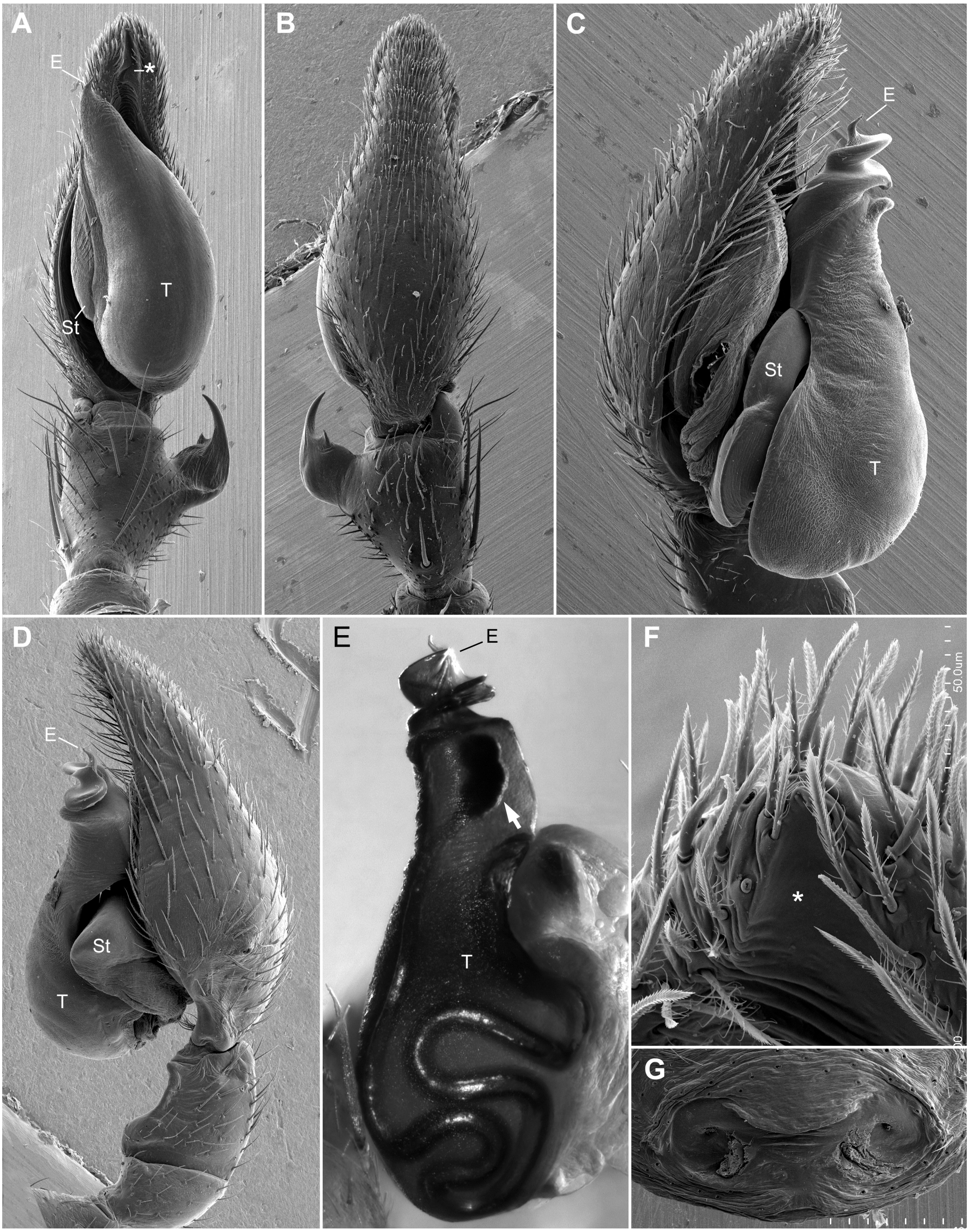


Fig. 158. Structures of left male palps and female epigyne of Castianeirinae (Corinnidae). **A.** *Medmassa semiaurantiaca* ventral, asterisk to cymbial apical groove. **B.** Same, dorsal. **C.** *Castianeira trilineata* prolateral. **D.** Same, retrolateral. **E.** Same, ventral, arrow to sclerotized bulb on sperm duct. **F.** Same, tip of cymbium, ventral, asterisk on cymbial apical groove. **G.** Same, epigyne, showing spiral ridges complementary to screw in male embolus.

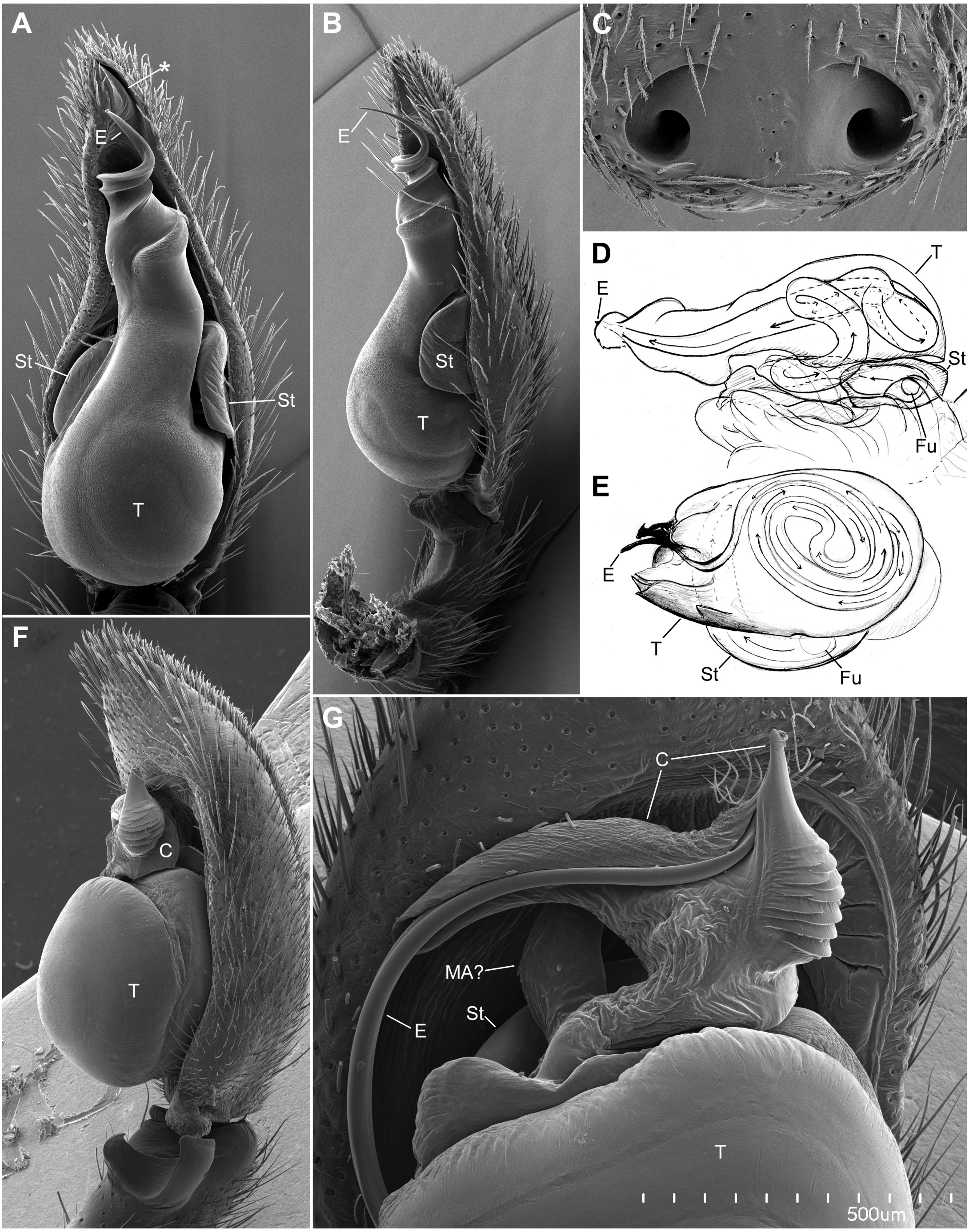


Fig. 159. Structures of left male palps and female epigyne of Castianeirinae and Corinninae (Corinnidae). **A.** *Copa flavoplumosa* ventral, asterisk to cymbial apical groove. **B.** Same, prolateral. **C.** Same, epigyne. **D.** *Copa* sp. Analamazaotra, copulatory bulb expanded. **E.** *Falconina gracilis* copulatory bulb expanded, ventral. **F.** *Corinna bulbula* retrolateral. **G.** Same, detail of copulatory bulb, ventral, the process labeled "MA?" can be interpreted as a tegular projection instead.

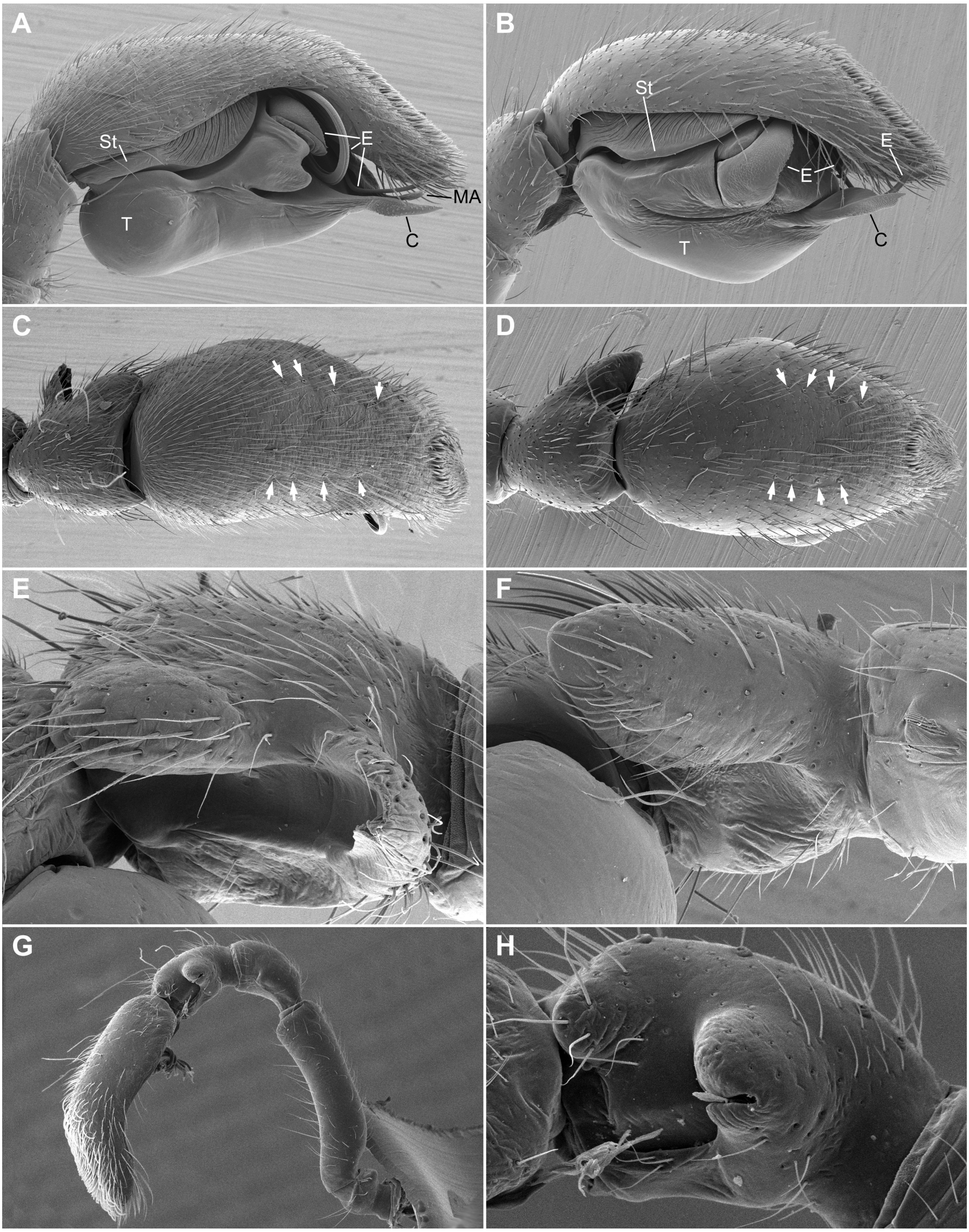


Fig. 160. Structures of left male palps of the *Teutamus* group (Liocranidae). **A.** *Jacaena* sp. prolateral. **B.** *Sesieutes* sp. prolateral. **C.** *Jacaena* sp., dorsal, arrows to trochobothrial bases. **D.** *Sesieutes* sp., dorsal, arrows to trochobothrial bases. **E.** *Jacaena* sp., tibia retrolateral. **F.** Same, tibia retrolateral. **G.** *Teutamus* sp. retrolateral. **H.** Same, tibia.

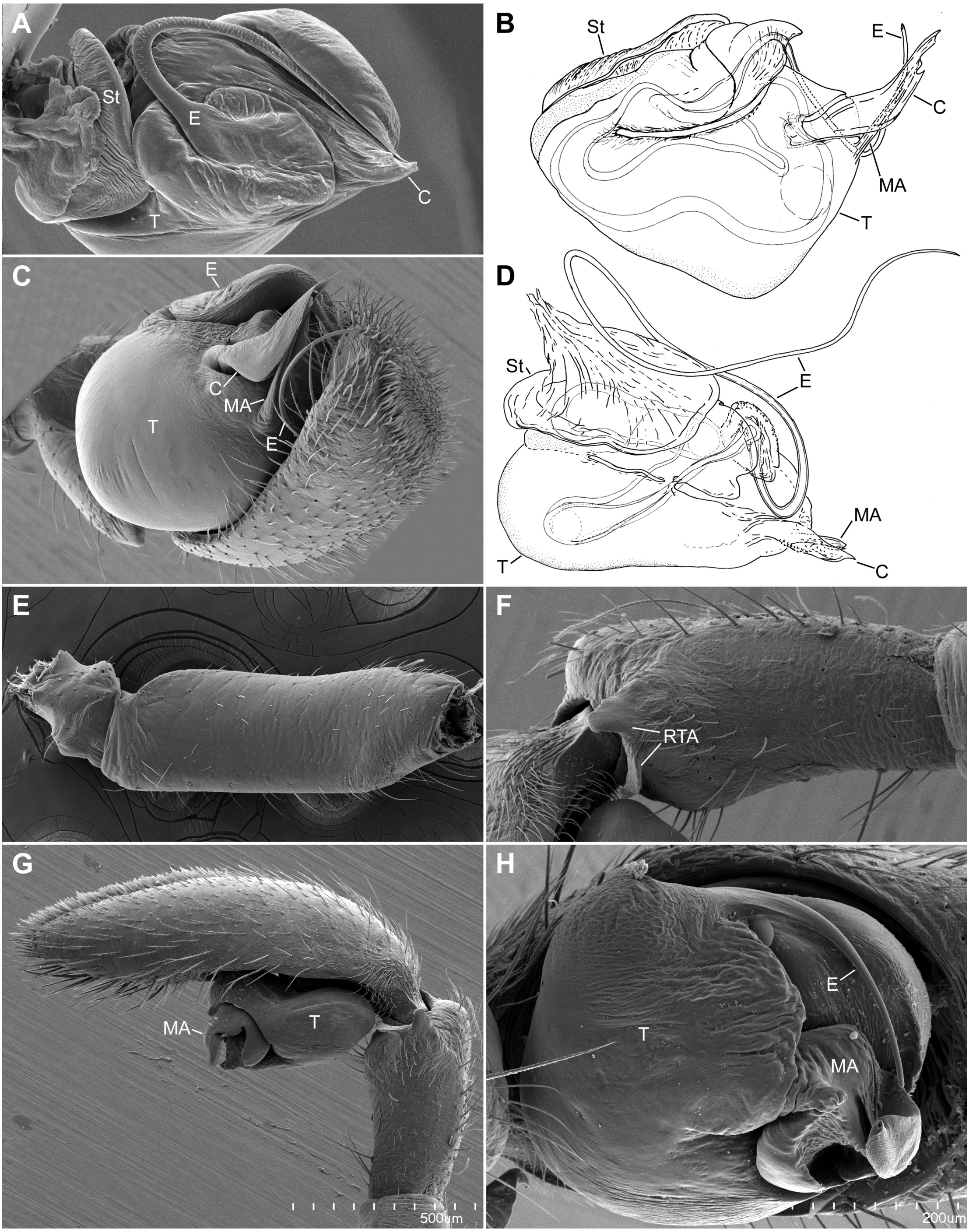

A
St
E
T
C
B
St
E
C
MA
T
C
E
C
MA
T
E
D
St
E
E
MA
T
C
E
F
RTA
G
MA
T
500um
H
E
T
MA
200um

Fig. 161. Structures of left male palps of the *Teutamus* group (Liocranidae). **A.** *Teutamus* sp., copulatory bulb dorsal-apical. **B.** *Sesieutes* sp., copulatory bulb prolateral-ventral. **C.** Same, palp apical-ventral. **D.** *Jacaena* sp., copulatory bulb prolateral. **E.** Same, femur prolateral. **F.** *Oedignatha* cf. *jocquei*, tibia retrolateral. **G.** Same, palp retrolateral. **H.** Same, copulatory bulb ventral.

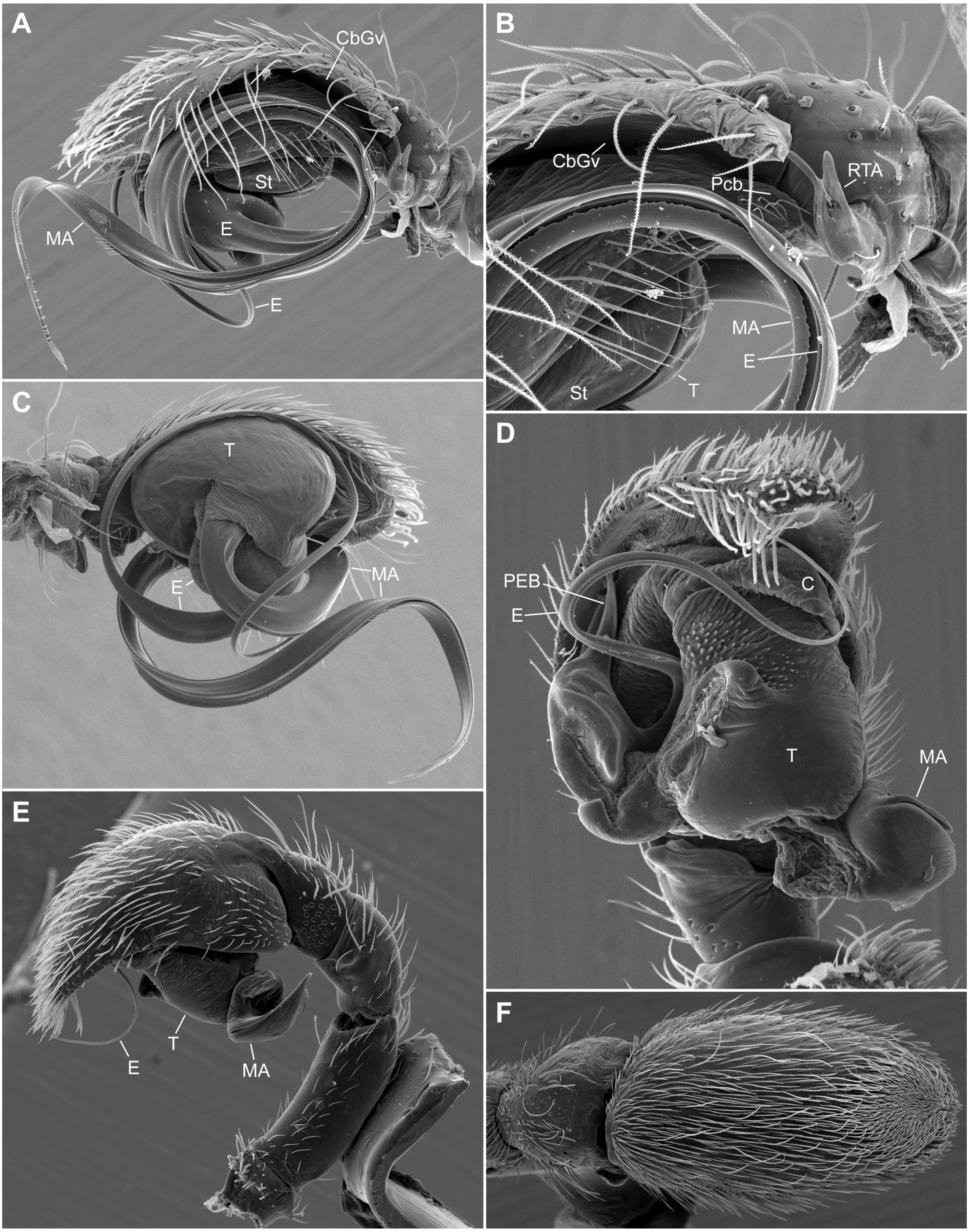

A
CbGv
St
MA
E
E
B
CbGv
Pcb
RTA
MA
E
St
T
C
T
E
MA
D
PEB
E
C
T
MA
E
E
T
MA
F

Fig. 162. Structures of left male palps. **A.** *Hortipes merwei* ("Corinnidae") retrolateral. **B.** Same, detail of tibia and cymbial groove. **C.** Same, ventral. **D.** *Xenoplectus* sp. ("Gnaphosidae") ventral. **E.** Same, retrolateral. **F.** *Austrachelas pondoensis* (Gallieniellidae) dorsal.

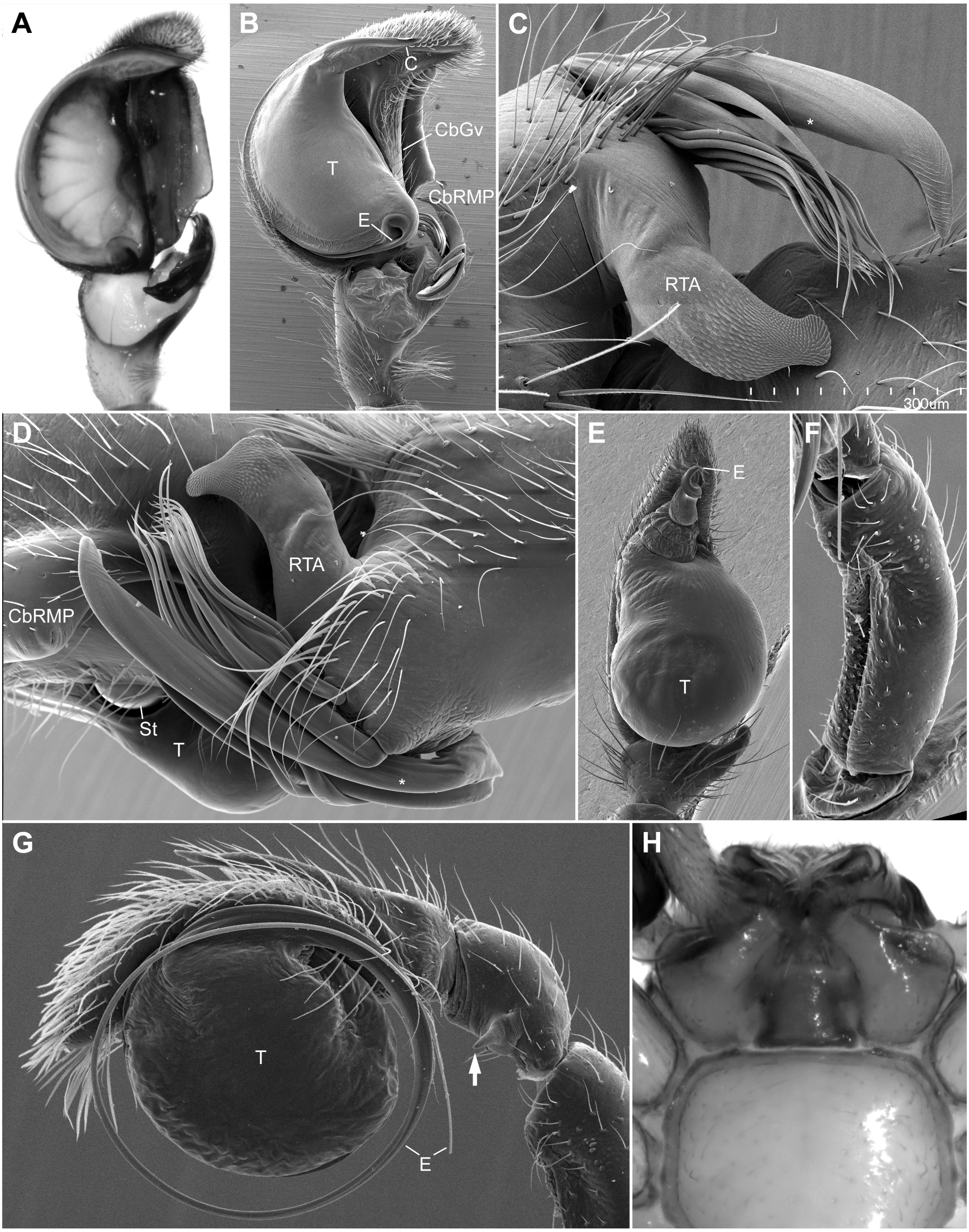


Fig. 163. Structures of left male palps and endites of Trachelidae. **A.** *Paccius* cf. *scharffi* ventral. **B.** Same. **C.** Same, tibial apophyses and modified setae, dorsal, asterisk on modified seta with canal. **D.** Same, retrolateral, asterisk on modified seta with canal. **E.** *Trachelas mexicanus* ventral. **F.** Trachelidae ARG, femur retrolateral. **G.** Same, palp retrolateral, arrow to retrolateral apophysis on patella. **H.** Same, endites ventral.

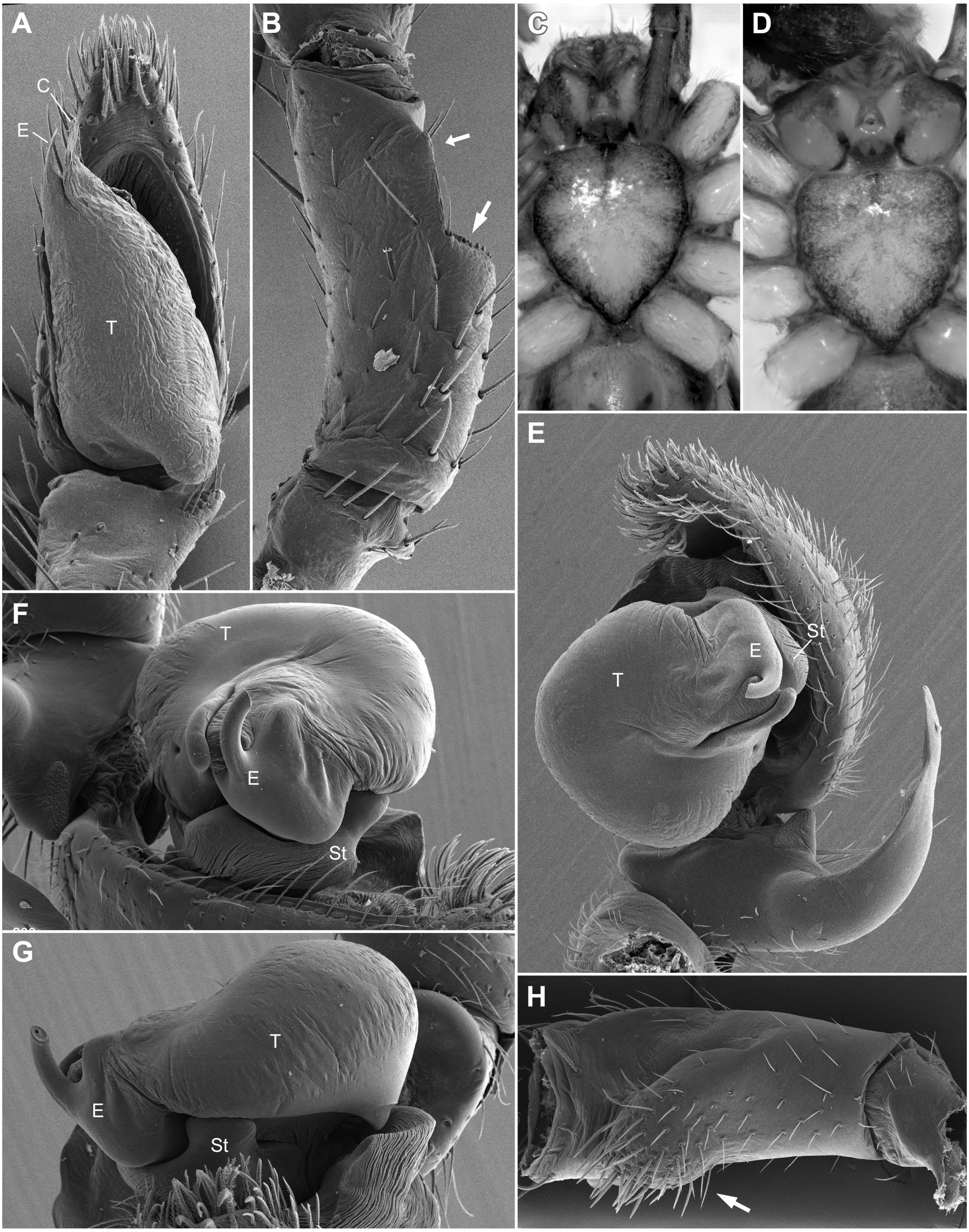


Fig. 164. Structures of left male palps and endites of Phrurolithidae. **A.** *Drassinella gertschi* ventral. **B.** Same, femur prolateral, lower arrow to femoral ventral median apophysis, upper arrow to ventral apical apical apophysis. **C.** *Phrurolithus festivus* female endites and sternum. **D.** Same, male, showing enlarged endites. **E.** Same, palp, retrolateral. **F.** Same, copulatory bulb apical. **G.** Same, prolateral. **H.** Same, femur ventral, arrow to femoral ventral median apophysis.

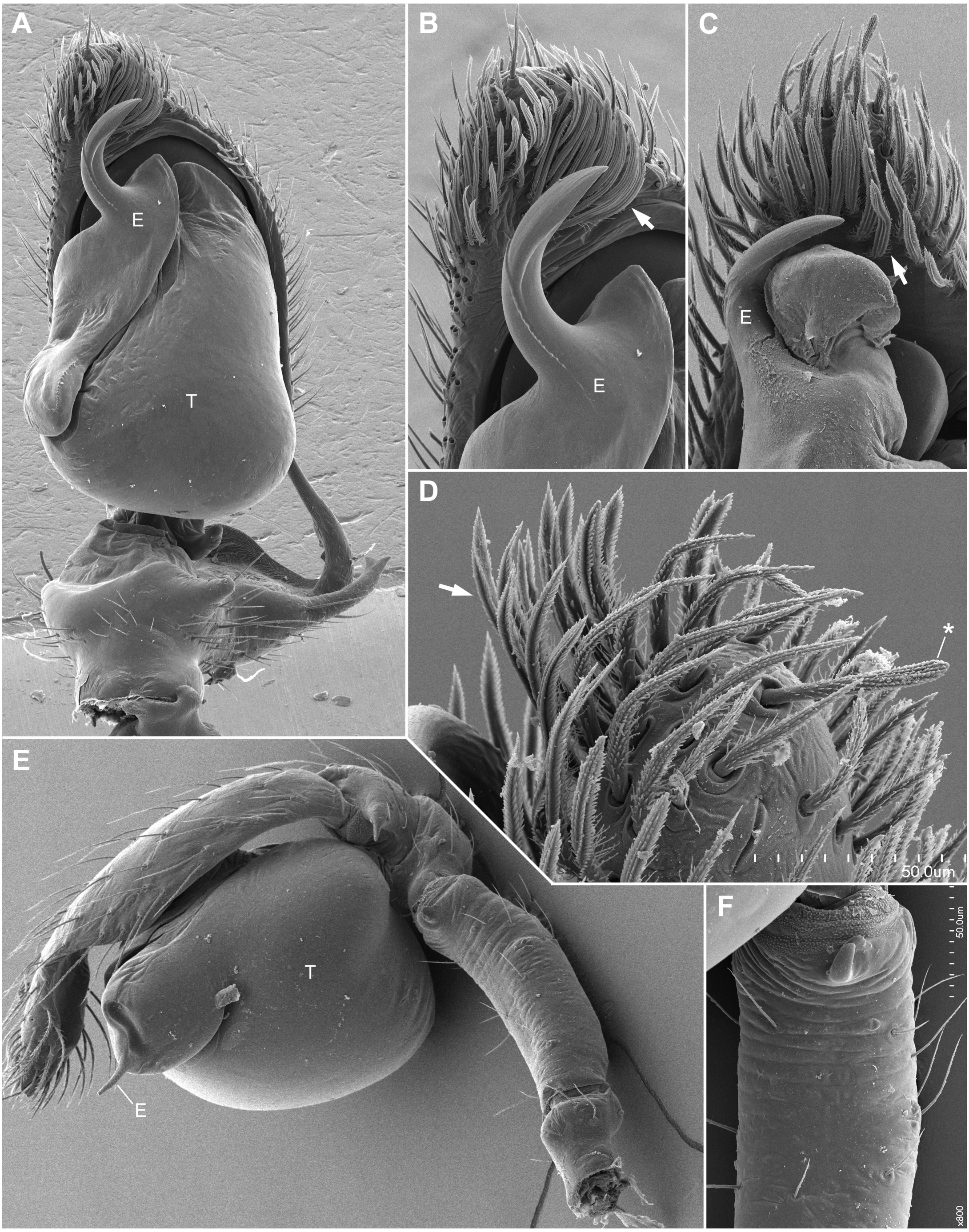


Fig. 165. Structures of left male palps and endites of Phrurolithidae, arrows to thick setae on cymbium. **A.** *Otacilia* sp. ventral. **B.** Same, detail of embolus and tip of cymbium. **C.** *Phrurotimpus alarius* ventral, detail of embolus and tip of cymbium. **D.** Same, tip of cymbium prolateral, asterisk to thick seta on cymbium tip. **E.** *Orthobula calceata* retrolateral. **F.** Same, distal half of femur, ventral.

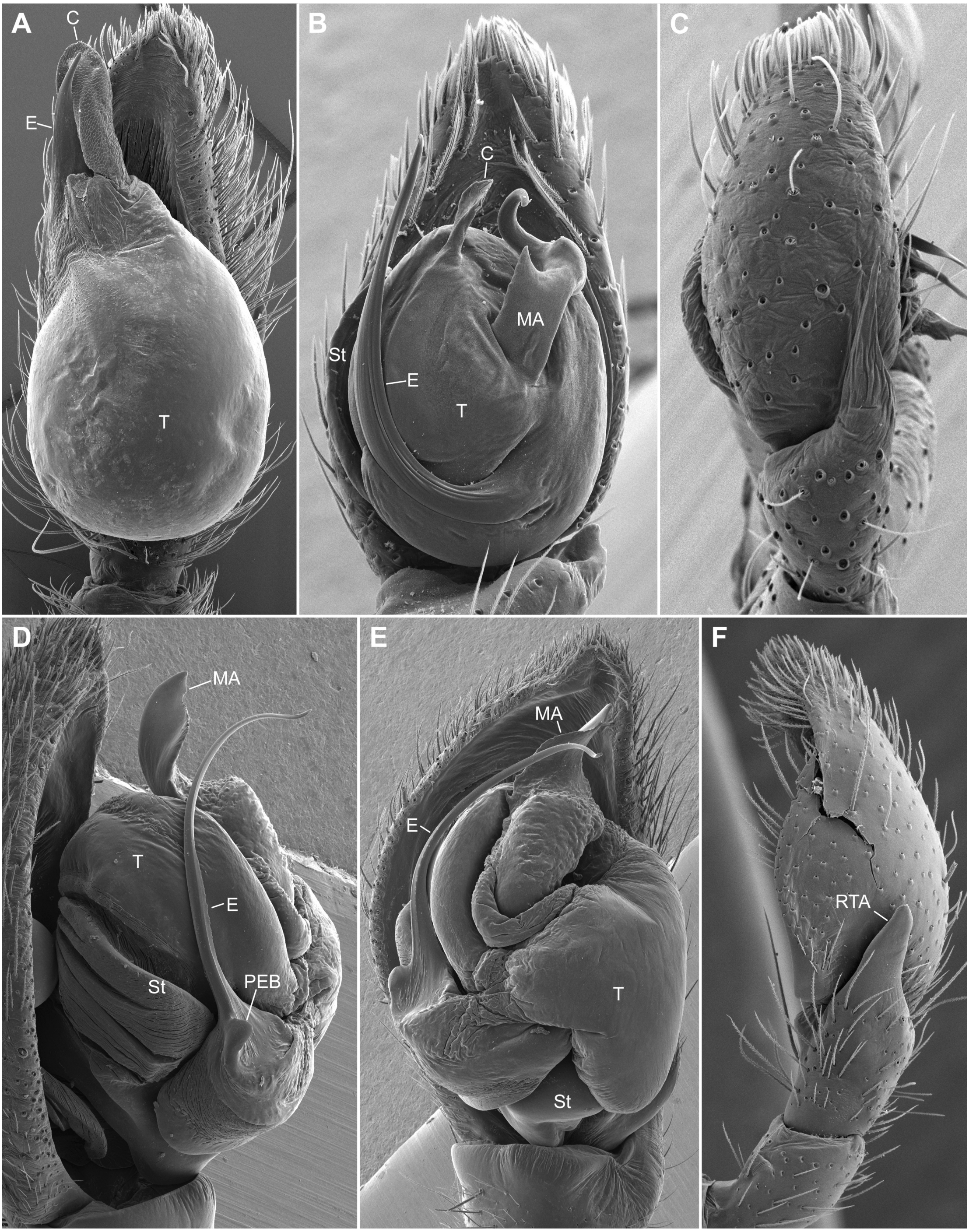


Fig. 166. Structures of male palps and endites of Gnaphosoidea. **A.** *Lampona cylindrata* (Lamponidae) left, ventral. **B.** *Lygromma* sp. (Prodidomidae) left, ventral. **C.** *Neozimiris pubescens* (Prodidomidae) right, dorsal. **D.** *Gnaphosa taurica* (Gnaphosidae) left, prolateral. **E.** Same, ventral. **F.** *Camillina calel* (Gnaphosidae) left tibia and cymbium, retrolateral.

sclerites are fused in a single piriform bulb (fig. 139A). The most conserved sclerites define the main divisions or sections of the copulatory bulb.

BASAL DIVISION OF COPULATORY BULB: The basal division spans between the basal and median hematodochae. It includes the subtegulum, and within it, the blind end of the spermophore, called the *fundus*.

MEDIAN DIVISION OF COPULATORY BULB: The median division spans between the median and terminal hematodochae. It includes the tegulum, and may have a conductor and median apophysis attached to it. The spermophore runs through the tegulum.

EMBOLIC DIVISION OF COPULATORY BULB: The embolic division spans all structures distal to the median division, articulated to the tegulum by a terminal hematodocha. It includes the intromittent structure with the sperm outlet, called the *embolus*. In some groups there is an intermediate sclerite, the radix, between the embolus and tegulum, with the spermophore passing through it.

304. Endites sexually dimorphic: 0. Not dimorphic. 1. Male endites with distal ectal projection (Ramírez, 2003: fig. 96B). 2. Male endites basally globose (compare fig. 164C, D). 3. Male endites with ectal-anterior concavity (fig. 163H). COMMENTS: *Cybaeodamus*: male endites more markedly depressed (scored 0). *Doliomalus*: just thinner in male (scored 0). *Plexippus*: not protruding (scored 0).

305. Male palpal femur ventral basal apophysis: 0. Absent (fig. 160G, 161E, 162E). 1. Present (fig. 140H; Opell, 1979: fig. 7). This is character 3 in Scharff and Coddington (1997). COMMENTS: *Uloborus*: one large, one small, not considered homologous with the median or apical processes (scored 1).

306. Male palpal femur ventral median apophysis: 0. Absent. 1. Present (figs. 140I, 152F, 164H). COMMENTS: *Paccius*: only a faint longitudinal ridge (scored 0). *Jacaena*: only a swelling (scored 0). *Galianoella*: the apical ridge-groove (scored 1).

307. Male palp femur ventral apical apophysis: 0. Absent. 1. Present (fig. 165F). The apical apophysis can cooccur with the median one (figs. 164B, 165E). COMMENTS: *Psechrus*: with thicker setae (scored 0). *Trachelas minor*: an apical lip fitting the patellar apophysis may be homologous with the apical apophysis (fig. 140G) (scored 01). *Drassinella*: simple process united to the median one by a ridge (scored 1). *Orthobula*: hook (scored 1).

308. Male palp femur ventral longitudinal groove: 0. Absent. 1. Present (fig. 163F).

309. Male palp patella dorsal apophysis: 0. Absent. 1. Present. COMMENTS: *Anyphaena*: shallow apical sclerotization (scored 01).

310. Male palp patella retrolateral apophysis: 0. Absent. 1. Present (figs. 140G, 157D, 163G). COMMENTS: *Clubiona*: absent in *Clubiona pallidula*, but present in other species (e.g., *Clubiona* cf. *maritima*) (scored 0).

311. Male palp retrolateral tibial apophysis (RTA): 0. Absent (figs. 151C, 158D). 1. Present (figs. 161F, 166F). Here the broad homology of RTA includes the dorsal apical processes. In this study it was not possible to discern separate homology correspondences for a dorsal apical tibial apophysis, an RTA displaced to a dorsal position, or a dorsal subprocesses of a complex RTA. This resulted in the optimization of the RTA down to include titanoecids. COMMENTS: *Eresus*: ambiguous (scored 01). *Araneus*: A ventral rounded protuberance. Because of the rotation of the palp, the homology is provisional (scored 0). *Mimetus*: because of the rotation of the palp, the homology is provisional (scored 0). *Calacadia*: only the ventral ledge plus the basal knob (scored 1). *Cryptothele*: male palp from Benoit (1978) (scored 1). *Toxopsiella*: similar to that of *Cycloctenus*, although in dorsal position (scored 1). *Elaver*: apparently moved dorsal (scored 1). *Trachelopachys*: should be the dorsal one (scored 1). *Paccius*: the dorsal branch only, the more ventral with canal is a modified seta (fig. 163C, D) (scored 1). Cf. Liocranidae LIB: thin spine as long as the cymbium, in dorsal position (scored 1). *Hortipes*: a trichobothria on the RTA! (fig. 162B) (scored 0). *Lygromma*: two processes (scored 1). *Legendrena*: if only one dorsal, then RTA (scored 1). *Odo bruchi*: a strong macroseta coming out of a retrolateral basal mound (scored 0). *Hovops*: palp provisionally scored from images by José Corronca (in litt.), from several species (scored 1). *Epidius*: in ventral-retrolateral position (scored 1). *Thomisus*: several setae with extremely enlarged, dark, protruding sockets (scored 1). *Aphantochilus*: tibia extremely short (scored 1).

312. RTA position: 0. Apical (fig. 166F). 1. Medial or basal (fig. 151A). COMMENTS: *Neoramia*: complex, apical and median apophyses (scored 01). *Metaltella*: both (scored 01). *Calacadia*: both (scored 01). *Macrobunus*: apical and median branches (scored 01). *Storenomorpha*: all sides of tarsus (scored 01). *Senoculus*: basal (scored 1). *Procopius*: one apical, one basal (scored 01). *Phrurolithus*: all retrolateral faces (scored 01). *Phrurotimpus*, *Otacilia*: all retrolateral faces (scored 01). *Orthobula*: tibia very short (scored 0). *Hortipes*: tibia short (scored 0). *Teutamus*: two branches (scored 01). *Jacaena*: two branches (scored 01). *Sesieutes*: both, similar as in *Jacaena* (scored 01). Cf. Gnaphosoidea TEX: short tibia (scored 01). *Xiruana*: both (scored 01). *Paravulsor*: two branches, one more basal (scored 01).

313. RTA articulation: 0. RTA fixed, base sclerotized. 1. RTA articulate through membranous insertion. See comments under character 317. COMMENTS: *Titanoeca*: it expands partially in KOH (scored 1).

314. RTA apical internal file: 0. Absent. 1. Present (figs. 143C, 151B, F, 152G). Lehtinen (2003: figs. 23, 25) also found files in the RTA of species of *Runcinia, Misumenops,* and *Henricksenia*. COMMENTS: *Dictyna*: well spaced, irregular striations (Griswold et al., 2005 176E) (scored 01). *Senoculus*: thick striations (scored 1). *Neato*: not seen with stereomicroscope (scored 0). *Corinna*: a reticulate surface on one of the branches (scored 0). *Brachyphaea*: entire surface with longitudinal ridges, including the internal side (fig. 157B, C) (scored 1). *Camillina*, *Apodrassodes*: a few apical ridges (scored 01). *Lamponella, Pseudolampona*: observed in clove oil and compound microscope (scored 0). *Strotarchus*: irregular grains (scored 0). *Ciniflella* BRA: file more extended than in Thomisidae (scored 1). *Polybetes*: aligned cusps (scored 1). *Epidius*: not found with compound microscope (scored ?). *Aphantochilus*: internal side of RTA not examined (scored ?).

315. RTA sclerotization: 0. All sclerotized. 1. With membranous area (figs. 145A, 163A, B). COMMENTS: *Desis*: canal membranous (scored 1). *Macrobunus*: central, dorsal, and ventral unsclerotized areas (scored 1). *Brachyphaea*: at the base, also surrounding all ventral processes (scored 1). *Paccius*: around the base of the modified seta (scored 1). *Phrurolithus*: internal membranous patch (scored 1). *Jacaena, Teutamus*: canal not sclerotized (scored 1). *Miturga* cf. *lineata*: with a ventral lobe not sclerotized (scored 1). *Teminius*: the canal area is membranous (scored 1). *Systaria*: internal side opposing cymbium, canal area membranous (scored 1). *Zora*: checked with stereomicroscope (scored 0). *Tibellus*: ventral membranous ridge extending into apophysis (scored 01). Sparianthinae VEN: between the pilose lobe and the complex apophysis (scored 1). *Titanebo*: membranous area extending into ventral branch of apophysis (scored 01).

316. RTA with canal: 0. Canal absent. 1. Canal present (figs. 142E, 146B, 160E, H). COMMENTS: *Toxopsiella*: canal not well marked (scored 01). *Brachyphaea, Mandaneta*: canal on ventral hook (scored 0). *Sesieutes*: similar morphology as in *Jacaena*, but canal very shallow (fig. 160F) (scored 0). *Paccius*: canal on the modified seta (scored 0). *Zora*: canal not well defined, but very similar in general shape to the RTA of *Mituliodon* (scored 01). *Selenops*: dorsal side of major RTA branch with incomplete canal (scored 01). *Anyphops*: a wide canal but not as in miturgids (scored 0).

317. Male palpal tibia gland: 0. Absent. 1. Present, discharging through a dorsal or retrolateral tibial apophysis. Described in Compagnucci and Ramírez (2000: 203) for macrobunine amaurobiids, and Wanless (1979, 1984, 1987) for a few genera of spartaeine salticids. The apophysis may be fixed or movable, with an articulated base. None of the amaurobiids, salticids, or any other terminal in this analysis bears a tibial gland discharging through tibial apophyses. See also character 313. COMMENTS: cf. Liocranidae LIB: not seen after clarification, RTA tip not perforated (scored 0).

318. Male palp tibia dorsal basal process: 0. Absent. 1. Present (figs. 140A, 144C). Here only the basal dorsal process is scored separately from the RTA. Other more apical dorsal processes are considered part of the RTA (see char. 311). The process identified by Harvey (1995) as an RTA displaced dorsally (in

Nicodamus and *Megadictyna*) is here considered a basal dorsal process. Scoring the dorsal basal process in nicodamids as an RTA only changes the tree by making Nicodamidae paraphyletic, and tracing the RTA origin back to the common ancestor of nicodamids and the RTA clade. COMMENTS: *Storenomorpha, Galianoella*: the tibia is too short to decide between apical and proximal (scored 01).

319. Male palp tibia dorsal basal process conformation: 0. Simple or absent (fig. 144C). 1. Complex (fig. 140A). In this dataset the complex condition is present only in the nicodamids *Nicodamus* and *Megadictyna*, and they look very similar to each other (scored 1).

320. Male palp tibia ventral apical apophysis: 0. Absent, simple swelling, or part of RTA complex. 1. Present, well defined (figs. 142H, 147B, 152A, C, G, 157A, B, E). The broad homology of the ventral apical apophysis is applied only to well-defined processes, separated from the RTA. Several instances of ventrally swollen tibiae were not considered as apophyses (see comments below). The hook-shaped ventral process of the thomisid *Boliscus* fits on a tegular ridge (fig. 152G). Huber (1995a) showed that in *Misumenops tricuspidatus* the ventral hook guides the rotation of the tegulum produced by hematodochal expansion. The general correspondence between the ventral apophysis and the ridges in the tegulum suggest that this function may be widespread in higher thomisids. COMMENTS: *Araneus*: A ventral rounded protuberance. Because of the rotation of the palp, the homology is provisional (scored 0). *Neoramia*: only an inflated margin (scored 0). *Stiphidion*, *Calacadia*, *Desis*, *Badumna*, *Metaltella*: the straight ledge forming a canal is considered part of the RTA complex, as in Griswold et al. (2005) *Oxyopes*: a hook like those of thomisids (fig. 142H) (scored 1). Cf. *Medmassa* THA: only a round elevation close to the RTA base (scored 0). *Castianeira*: a longitudinal ridge (scored 0). *Trachelopachys*: apical retrolateral-ventral (scored 0). *Pseudocorinna*: prolateral-ventral simple prong (scored 1). *Paccius*: the more ventral process is a modified seta (fig. 163D) (scored 0). *Brachyphaea*: a ventral hook with a canal (fig. 157B) (scored 1). *Procopius*: the ventral-retrolateral process interpreted as an RTA; there is also a ventral-basal process (scored 0). *Mandaneta*: a flat projection and a small hook with canal and reticulate texture (scored 1). *Neoanagraphis*: just raised articulation margin (scored 0). *Phrurolithus*: extensive membranous articulation with swelling border (scored 0). *Legendrena*: all ventral side bulbous, similar as in *Phrurolithus* (scored 0). *Ammoxenus*: ventral and prolateral margin extended in a cup, receiving the copulatory bulb (scored 0). *Cheiramiona*: similar as in *Eutichurus*, but the articulating membrane arises just on the border (scored 01). *Eutichurus*: flat process, not hooked (scored 1). *Systaria*: swelling all around the tibia (scored 0). *Raecius*: interpreted as a ventral branch of the RTA (scored 0). *Philodromus*: *P. californicus* similar as in thomisids, *P. aureolus* broader process; perhaps with conductor function (scored 1). *Geraesta*: reduced but evident (scored 01). *Strophius*, *Aphantochilus*, *Tmarus*: retrolateral hook (scored 1). *Epidius*: Interpreted as an RTA. The apical ventral macrosetae are reminiscent of those found in *Cebrenninus* at base of RTA, but the position is different (scored 0). *Boliscus*: hook shaped, fitting ridge in tegulum (fig. 152G) (scored 1).

321. Male palp tarsus muscle M29: 0. Present. 1. Absent. See Huber (2004) and Griswold et al. (2005: char. 128). In this dataset M29 is expected to have the same distribution as M30 (Griswold et al., 2005: char. 129); differences were reported in Hersiliidae and *Uroecobius* by Huber (1994, 2004). COMMENTS: *Hypochilus*: the M29 partly originates in the patella (Huber, 2004) (scored 0). *Filistata*: from Huber (2004), after *Kukulcania hibernalis*. *Eresus, Oecobius, Homalonychus*: from Huber (1994) (scored 1). *Uloborus*, *Araneus*, *Huttonia*, *Dictyna*: after Bernhard Huber (in litt.) in Griswold et al. (2005: char. 128). *Nicodamus*: some unspecified Nicodamidae examined by Huber (1994) (scored ?). *Miturga* cf. *lineata*: not observed, but absent in an unspecified Miturgidae (Huber, 1994) (scored ?).

322. Orientation of cymbium relative to bulb: 0. Dorsal. This is the general condition in the RTA clade (fig. 147A). 1. Mesal. Araneids have the copulatory bulb facing outward, with a mesal cymbium (fig. 141F) (Griswold et al., 1998: char. 2). 2. Basal. Hypochilids and filistatids have the copulatory bulb apical in the male palp (fig. 141A, E). COMMENTS: *Uloborus*, *Orthobula*, Trachelidae ARG, *Hortipes*: intermediate (scored 01).

323. Cymbial tip ventral groove: 0. Absent (fig. 153C). 1. Present. The cymbium has a ventral apical smooth groove that usually holds the embolus in a resting position (figs. 156B, 158F). This character was proposed as a synapomorphy for Anyphaenidae except Malenellinae (Ramírez, 1995, 2003). In this dataset it also occurs elsewhere, including as a synapomorphy for Castianeirinae. COMMENTS: *Filistata*: no cymbial tip (scored ?). *Mimetus*: very modified (scored 01). *Huttonia*: very wide, more evident in other species (Forster and Platnick, 1984: fig. 277) (scored 1). *Storenomorpha*: Also with canaliculate hairs, see Jocqué (1991: figs. 39, 40). He suggested that those hairs might produce the mating plug (scored 1). *Zoropsis*, *Pseudoctenus*: ambiguous, border too short (scored 01). Cf. *Medmassa* THA: only concave and devoid of hairs (scored 0). *Castianeira*: not so markedly notched (scored 1). *Ammoxenus*: very wide notch (scored 01). *Uliodon*, *Liocranoides*, *Austrachelas*: slightly notched (scored 01). *Xiruana*: glabrous, sclerotized groove (scored 1). *Ciniflella* BRA: perhaps a soft fold (scored 0). *Eusparassus*: groove with setae (scored 1). *Hispo*: perhaps slightly notched (scored 01).

324. Cymbium dorsal chemosensory patch: 0. Absent, chemosensory setae sparsely distributed (fig. 140B). 1. Present, chemosensory setae in a dense patch (figs. 142C, 149C, 155E, 162F). Often described as a "cymbial dorsal scopula," this patch is formed by chemosensory setae (Griswold et al., 2005: char. 113). As can be reconstructed by the comments below, the chemosensory patch occurs scattered in many families, often with poorly defined limits. COMMENTS: *Acanthoctenus*, *Vulsor*, *Ctenus*, *Falconina*, *Paradiestus*: borders not well defined (scored 1). *Medmassa*: not well defined, dorsodistal transverse bands (fig. 158B) (scored 0). *Paccius*: dense, not well-defined borders (scored 1). *Procopius*: borders not defined (scored 0). *Apostenus*: not dense but definite (scored 1). Cf. Liocranidae LIB: prolateral to a cymbial dorsal canal fitting the RTA (scored 1). *Toxoniella*, *Gayenna*, *Macerio*, *Miturga* cf. *lineata*, *Systaria*: not well delimited (scored 0). *Phrurotimpus*: larger blunt apical seta (scored 0). *Malenella*: the blunt setae (Ramírez, 1995) are chemosensory, similar to those below the claws (scored 1). *Cheiracanthium*: present but not well defined (scored 1). *Mituliodon*: a few sparse, thick, short setae (scored 0). *Strotarchus*: not well defined, but many setae present (scored 1). *Zora*: a bunch of thick setae (scored 0). *Xenoctenus*: tenent setae (scored 0). *Liocranoides*: small patch (scored 1). *Titanebo*: distal ring (scored 0).

325. Cymbial apex extension beyond alveolus: 0. Extending beyond distal margin of alveolus (fig. 148B). 1. Short, wide, not extending beyond distal margin of alveolus (figs. 142B, 143E, 144A). COMMENTS: *Hypochilus*, *Filistata*, *Ariadna*: no alveolus (scored ?). *Araneus*: flat, wide (scored 1). *Huttonia*: very small alveolus (scored 01). *Eriauchenius*: reduced cymbium (scored 01). *Apostenus, Ciniflella* ARG, *Boliscus, Thomisus*: intermediate (scored 01). *Raecius*: not in *R. asper* (scored 1).

326. Cymbial apical ventral setae: 0. Sparse, regular setae (figs. 147E, 153C). 1. Bunch of thick setae. These setae may be ridged (fig. 165B, C), or dark and erect (figs. 147D, 148B, C, E, F). A bunch of thicker or darker setae may occur just distad of the apical margin of the cymbial alveolus. COMMENTS: *Donuea*: similar as in Phrurolithidae, but thin hairs (scored 0). *Trachelas mexicanus*, *Strotarchus*, *Ciniflella* BRA, *Polybetes*: some thick setae at the tip of cymbium (scored 0). *Micaria*: three macrosetae (scored 0). *Prodidomus*: some setae slightly similar as in Phrurolithidae, with slim base, slightly expanded, flattened apically (scored 0). *Neozimiris*: two thick setae toward prolateral side; *Zimiris* has several of these setae in similar position to that in Phrurolithidae (Platnick and Penney, 2004: figs. 4, 21) (scored 1). *Cheiramiona*: a bunch of long setae, but not as thick as in Phrurolithidae (scored 1). *Stephanopoides*: a few bottle-shaped chemosensory setae (scored 0).

327. Cymbial tip apical thick setae: 0. Absent. 1. Present (figs. 150D, 165D). A few terminals have only one thick apical seta (figs. 149E, 165D). COMMENTS: *Cryptothele*: not only apical (scored 1). *Ctenus*: some of the rakelike setae with very short thin tip (scored 01). *Pronophaea*: many short blunt setae (fig. 157G, H) (scored 1). *Liocranum*: intermediate (scored 01). *Ammoxenus*: there are macrosetae, but all over the cymbium (scored 01). *Phrurotimpus*: one, blunt (fig. 165D) (scored 1). *Otacilia*: at least one blunt, a second one may be broken (scored 1). Cf. Eutichuridae QLD, Eutichuridae MAD: one (fig. 149E) (scored 1). *Syspira*: as in most miturgids, with thick short setae, not so thick as in *Zora* (scored 1). *Xenoctenus*: mixed with the other setae (scored 1). *Griswoldia*: very thick (scored 1). *Heteropoda*: thick apical setae finely barbed, coordinately with cheliceral rake setae (scored 1). *Aphantochilus*: short macrosetae (scored 1).

328. Cymbial tip horn: 0. Absent, cymbial tip rounded (figs. 158F, 165D). 1. Present, cymbial tip ending in a cone (fig. 142J). In this dataset the horn is only present in *Senoculus* and *Thaida*.

329. Cymbial trichobothria: 0. Absent. 1. Present (figs. 160C, 166C).

330. Cymbial trichobothria rows: 0. One row, or single. 1. Several in two rows (fig. 160C, D). A potential synapomorphy of a group of South East Asian liocranids (*Teutamus*, *Sesieutes*, *Jacaena*), with multiple cymbial trichobothria in two rows. COMMENTS: *Badumna, Geraesta*: two in longitudinal line (scored 0). *Stiphidion, Metaltella*: one row (scored 0). *Calacadia*: one row proximally, much widened at the end (scored 01). *Medmassa*: marginal lines at each side (scored 1). *Teutamus*: five, dispersed, perhaps two irregular rows (scored 1). *Sesieutes*: eight, in two rows (scored 1). *Jacaena*: eight, in two rows (fig. 160C) (scored 1). Cf. Gnaphosoidea TEX: several, in more than one row, the images are not clear if in definite rows (scored 1). *Galianoella*: at least two rows, the median one with several trichobothria, seen in stereomicroscope (scored 1).

331. Retrolateral cymbial groove: 0. Absent. 1. Present (figs. 145F, 148D, 162A, B). COMMENTS: *Pimus*: small groove just at the margin, ventral (scored 0). *Mandaneta*: the bulb is swelling over a surface that looks like a flattened groove, with small setae on it (scored 01). *Neoanagraphis*: margin modified (scored 0). *Oedignatha*: absent in the species scored (fig. 161F), but present in *O. scrobiculata* (scans by R. Raven, in litt.) (scored 0). *Anagraphis*: widened, ventral, not on lateral pilose area (scored 0). *Ammoxenus*: longitudinal depression fitting large RTA (scored 01). Cf. Eutichuridae QLD, *Miturga* cf. *lineata,* Miturgidae QLD: only basal, superficial (fig. 149A) (scored 01). *Systaria*: fitting the RTA (scored 1).

332. Cymbial groove setae thickness: 0. Thin or absent (fig. 148D). 1. Thick setae (fig. 146B). COMMENTS: *Hortipes*: only thin setae (scored 0). *Oedignatha*: only thin setae, more aligned in *O. scrobiculata* (scans by R. Raven, in litt.) (scored 0). *Hortipes*: only thin setae (scored 0). *Miturga* cf. *lineata*: a few macrosetae, close to the apophysis (scored 01). *Teminius*: thick setae (scored 1).

333. Cymbial groove posterior extension: 0. Not extending beyond articulation with tibia (figs. 146B, 148D). 1. Extending in acute conductorlike process (figs. 147E, F, 149B–D). The morphology of the extended groove suggests that it may play a role in leading the embolus during expansion. COMMENTS: *Oedignatha*: present in *O. scrobiculata* (scans by R. Raven, in litt.) (scored ?). Cf. Eutichuridae QLD, *Cheiramiona*: a short cusp in that place (scored 0).

334. Cymbial retrobasal file: 0. Absent. 1. Present (Griswold et al., 2005: 12, fig. 183). See Griswold et al. (2005: 12). This is presumably a synapomorphy of Macrobuninae.

335. Cymbial retrobasal process (including the paracymbium): 0. Absent. 1. Present (figs. 140C, 142D, 159F, 165A). Here the retrobasal process arises independently in araneoids (*Araneus* + *Mimetus*), and several other groups of the RTA clade, including dionychans. For a discussion, see Griswold et al. (1998: 31). COMMENTS: *Hypochilus*: very different in morphology from other terminals, and separated from the alveolus (scored 1). *Megadictyna*, *Titanoeca*, *Clubiona*, *Castianeira*: excavated area (scored 0). *Nicodamus*: excavated area plus projecting border (scored 01). *Cyrioctea*: excavated area plus median projecting lobe (scored 01). *Cybaeodamus*: with basal membranous area inflated on KOH expansion (scored 1). *Zoropsis, Lauricius*: inconspicuous projecting base (fig. 143D) (scored 01). *Toxopsiella*: excavated area plus shallow projection (scored 01). *Creugas*: retrobasal process complex, interacting with the RTA (scored 1). *Falconina*: retrobasal process is complex, interacting with the RTA (scored 1). *Copa*: retrobasal complex slightly protruding, similar to that in *Corinna* (scored 01). *Mandaneta*: small, hidden by bulb (scored 0). *Apostenus*: very short lobe (scored 0). *Liocranum*: short lobe (scored 01). *Hortipes*: a prolongation of the cymbial groove (scored 1). *Oedignatha*: Excavated, just a short projection. Present in *O. scrobiculata* (scans by R. Raven, in litt.) (scored 0). *Micaria*: protruding border (scored 0). *Centrothele*: a process fitting the RTA is more dorsal than the paracymbial processes of other terminals (scored 0). *Austrachelas*: hole matching RTA (scored 0). *Neato*: excavated area fitting RTA and ventral low pilose mound (scored 0). *Trachycosmus*: excavated plus median bump (scored 01). *Fissarena*: excavated plus median lobe (scored 01). *Platyoides*: a large glabrous area and a small hole in front of the RTA (scored 0). *Ammoxenus*: shallow lobe (scored 0). Cf. Eutichuridae QLD: small mounds (scored 1). *Cheiracanthium*: the hook where the cymbial extends (scored 1). *Cheiramiona*: small conic process (scored 1). *Uliodon*: retrobasal process similar to that in *Corinna* (scored 1). *Zorocrates*: short projecting border plus retrolateral-dorsal bump (scored 01). *Selenops*: depressed area with shallow projection (scored 01). *Hovops*: other species may have, but not this one (scored 0). Sparianthinae VEN: excavated plus median bump (scored 01). *Heteropoda*: small knob (fig. 154E) (scored 01).

336. Cymbial retromedian process: 0. Absent. 1. Present, without a furrow (figs. 140C, 143D, 151E, 154A). 2. Present, forming a canal, conductorlike (includes the thomisid tutaculum) (fig. 152D, E). States are ordered. A few terminals have both a retrobasal and a retromesal processes (fig. 140C). COMMENTS: *Nicodamus*, *Pimus*: more dorsal (scored 0). *Cryptothele*: a simple mound, illustrated by Benoit (1978: fig. 3C) (scored 01). *Paccius*: there is a longitudinal furrow basal to the process, scored as a retrolateral cymbial groove (fig. 163B) (scored 1). *Agroeca*: very shallow mound (scored 01). *Trachelopachys*: shallow lobe, absent in other congeners (scored 01). *Gnaphosa*: intermediate, absent in other species (scored 0). *Apodrassodes*: a shallow mound (scored 1). *Meedo*, *Fissarena*: only a protuberance (scored 1). *Miturga gilva*: present, at the end of the groove (scored 1). *Aphantochilus*: intermediate, very thin (scored 12). *Plexippus*: shallow pilose lobe (scored 01).

337. Cymbium dorsobasal modifications: 0. Absent. 1. Projection (figs. 143B, 155D). 2. Transverse furrow (fig. 142I). COMMENTS: *Cyrioctea*: very slightly raised, continued from retrobasal concavity (scored 01). *Storenomorpha*, *Creugas*: a transverse furrow (scored 2). *Homalonychus*: funny protuberance fitting the RTA (scored 1). *Oxyopes*: a peculiar furrow fitting the dorsal tibial apophysis (scored 2). *Clubiona*: *Clubiona* cf. *maritima* with dorsal cymbial projection (scored 0). *Cocalodes*: two short macrosetae (scored 0).

338. Cymbium-tegulum fusion: 0. Free. 1. Fused. Some prithine filistatids have the cymbium partially fused to the tegulum (Gray, 1995; Ramírez and Grismado, 1997), and many Oonopidae show several degrees of fusion (e.g., Platnick and Dupérré, 2010). The fusion does not occur in this dataset.

339. Subtegulum transverse, distally crossing a piriform bulb: 0. Other bulb conformations. 1. Subtegulum transverse, crossing, visible from both sides (figs. 158D, 159A, 164F). The apical embolar section of some phrurolithids and castianeirines is delimited by a transversely placed subtegulum, visible from both sides. COMMENTS: *Creugas*: subtegulum L-shaped, with partially subdivided, more basal branch (scored 0). *Copa*: subtegulum mostly subdivided into two pieces (scored 1). *Medmassa*: intermediate (scored 01). *Otacilia*: intermediate between crossing and an apical cup (scored 01). *Eusparassus*: subtegulum mostly hidden, just visible at the center, through the loop of the embolus (scored 0). *Plexippus*: subtegulum a thin ring (scored 0).

340. Subtegulum-tegulum fusion: 0. Separate (figs. 139C, 141B). 1. Fused (fig. 141C, D). COMMENTS: *Hypochilus*: a thick articulation (scored 0). *Filistata*: In *Kukulcania* separated on one side, fused on the other (see also Huber, 2004: fig. 10). Interpreted as fused (scored 1). *Thaida*: I cannot see two separate sections (see also Huber, 2004: fig. 11) (scored 1). *Eresus*: a thick articulation (scored 0). *Huttonia*: the hematodocha commented in Forster and Platnick (1984) is the basal one (scored 1). *Donuea*: interpretation of palp very difficult, tentative (scored 0).

Hispo: it seems fused, but the tegulum is partially membranous (scored 01).

341. Subtegular locking lobe: 0. Absent (fig. 153B). 1. Present (figs. 143A, B, 156D, 164G). The subtegulum has a lobe, often fitting an opposing lobe on the embolar base. This character was originally proposed for some lycosoids by Griswold (1993), where the tegulum and subtegulum have lobes interlocking in the bulb when in resting position. The system was later reported in other families, and it was also found that the tegular lobe is the embolar base when the embolus is articulated (Griswold et al., 2005). Other locking mechanisms have been described in Theridiidae (median apophysis-cymbium; Agnarsson, 2004) and Nicodamidae (Griswold et al., 2005). In this dataset several terminals have an internal locking mechanism, exposed only after bulb expansion (e.g., in *Olbus*, Ramírez et al., 2001: fig. 47). In cycloctenids the subtegulum has a hole instead of a lobe, fitting the embolar lobe (fig. 142F). COMMENTS: *Oecobius*: see Baum (1972: fig. 62), it looks as if it has both tegular and subtegular locking lobes (scored 0). *Nicodamus*: plus a tegular lobe of another kind (scored 1). *Badumna*: absent, but there seems to be some internal ridges (scored 0). *Homalonychus*: subtegular lobe more like a hole (scored 1). *Vulsor*: on retrolateral side, entire bulb rotated (scored 1). *Ctenus*: similarly as in *Xenoctenus*, but hidden by the tegulum (scored 1). *Oxyopes*: at the base of the embolus, embolar lobe (scored 0). *Aglaoctenus*: the tegular notch harbors most of the subtegulum (scored 0). *Cycloctenus*: very similar to that of *Toxopsiella*, including hole in subtegulum (scored 0). *Toxopsiella*: impressive embolar lobe fitting in subtegular hole (fig. 142F) (scored 0). *Paccius*: very well defined, retrolateral (scored 1). *Mandaneta*: subtegular lobe fitting in a hole just below the median apophysis (scored 1). *Olbus*: internal locking, Ramírez et al. (2001: fig. 47) (scored 0). *Agroeca*: lobes tightly coupled (scored 1). *Phrurolithus*: embolar base fits lobe in subtegulum (fig. 164G) (scored 1). *Lampona*: not even internal locking (scored 0). *Centrothele*: there may be an internal locking (scored 0). *Meedo*: locking lobes visible in retrolateral view (scored 1). *Trachycosmus*, *Fissarena*: with internal locking mechanism with lobes on both tegulum and subtegulum, not close to the base of embolus (scored 0). *Desognaphosa*: a small locking lobe near embolus base (scored 1). *Teminius*: opposing embolar base (scored 1). *Syspira*: retrolateral-basal (scored 1). *Xenoctenus*: basal (scored 1). *Uliodon*: matching embolar lobe (scored 1). *Ciniflella* BRA: internal locking (scored 0). *Anyphops*: Subtegular lobe plus hole. There are additional tegular-subtegular locking lobes on the other side, as in *Nicodamus* (scored 1). *Tmarus*: as in *Nicodamus*, both locking lobes not related with embolar base (scored 0). *Holcolaetis*: subtegular lobe just shallow depression (scored 01). *Portia*: base of embolus fitting shallow depression and lobe in subtegulum (scored 01). *Galianoella*: plus a dorsal lobe locking on the cymbium! (scored 1).

342. Tegular (embolar base) locking lobe: 0. Absent (fig. 153B). 1. Present. The embolar base has a lobe, often fitting an opposing lobe on subtegulum (fig. 143A, B). See Griswold et al. (2005: char. 116). COMMENTS: *Nicodamus*: with a lobe arising close to the beginning of sperm duct, not at the base of embolus (scored 0). *Metaltella, Calacadia*: the anterior sclerotized hook, unmatched (scored 01). *Macrobunus*: the tegular lobe is ventral to the embolus, considered as an embolar process (scored 0). *Homalonychus*: lobe at base of embolus. *Zoropsis*: embolar lobe (scored 0). *Pseudoctenus*: embolar base lobe conspicuously protruding (scored 0). *Trachelas mexicanus*: a projecting triangle before embolar base (scored 0). *Paccius*: very well defined, retrolateral (scored 1). *Agroeca*: lobes tightly coupled (scored 1). *Phrurolithus*: embolar base fits lobe in subtegulum (scored 1). *Xenoplectus*: The tegular lobe is on a partially separated part where the embolus arises. It might be part of the embolar base (scored 1). Cf. *Moreno* ARG: embolar base (scored 1). *Vectius*: there is a locking lobe, but not clear if part of the embolus (scored ?). *Fissarena*: a tegular lobe, but not so close to the embolus insertion (scored 01). Miturgidae QLD: the base of the embolus is protruding, although not locking anything (scored 01). *Miturga gilva*: there is a lobe there, but not matching the subtegular one (scored 0). *Syspira*: embolus free, an irregular separate lobe from tegulum (not embolar base) in front of that of subtegulum (scored 0).

Uliodon, Raecius: the base of the embolus (scored 1). *Xenoctenus*: basal, tegular lobe at the base of long embolus (scored 1). *Liocranoides*: large tegular lobe at embolus base (scored 1). Sparianthinae VEN: a not well-defined tegular lobe at base of embolus (scored 01). *Lauricius*: embolar lobe, because embolus is free (scored 1). *Holcolaetis*: basal lobe (scored 1).

343. Tegular distal division at embolar base: 0. Absent. 1. Present. In *Xenoctenus* and related genera the tegular region where the embolus arises is delimited from the rest of the tegulum by a membranous area, and extends forward. This division may be small (fig. 150A) or very large, with a furrow leading the embolus (fig. 150B, C, E). This structure was proposed by Silva Davila (2003: fig. 18, char. 38, "*Odo*-like" sclerotized tegular process) as a synapomorphy joining some *Xenoctenus* and *Odo* species. Because it is not clear whether this region belongs to the tegulum or is instead a basal embolar process, character 351 was scored as uncertain for the terminals having this structure (the *Xenoctenus* group: *Xenoctenus*, *Odo bruchi*, *Paravulsor*). In *Lyssomanes* the tegulum has a deep and narrow transverse furrow arising close to the embolus base (fig. 155A), thus delimiting a thin strip of tegulum somehow similar to the configuration found in the *Xenoctenus* group (scored 01) (see char. 344).

344. Tegular notches: 0. None. 1. Amaurobioidinae-like. The tegulum has a deep basal indentation, occupied by the median hematodocha (fig. 156C). 2. Lycosidae-like. The tegulum has a basal indentation, occupied by the subtegulum (fig. 142G). 3. Basal transverse furrow. The tegulum has deep and narrow transverse furrow arising close to the embolus base (fig. 155A). COMMENTS: *Thaida*: tegulum just a sclerotized band (scored ?). *Oxyopes*: most of the tegulum is membranous (scored 0). *Strotarchus*: the median hematodocha is well exposed at the base of the tegulum, in ventral view (scored ?). *Liocranoides*: large central membranous area extending posteriorly, mesal to trajectory of sperm duct (scored 0). *Plexippus*: unsclerotized area projecting basally (scored 0).

345. Proximal sperm duct constriction: 0. Absent. The proximal section of the sperm duct not constricted. 1. Present, near fundus. The proximal section of the sperm has a narrow constriction (Huber, 1994: fig. 1). According to Huber (1994) this is a potential synapomorphy of *Oecobius* and *Uroctea.* COMMENTS: *Eresus*: from Huber (1994) (scored 0). *Oecobius*: from Huber (1994) (scored 1). *Storenomorpha*: too dark (scored ?). *Ctenus*: internal, not clarified (scored ?). *Dolomedes*: from Sierwald (1990) (scored 0).

346. Sperm duct distal thickness: 0. Gradually tapering, or thinned before embolus (fig. 159D). 1. Thick sclerotized apical bulb, described as "sclerotized area on distal reservoir" by Bonaldo (2000: figs. 90–105) (see also fig. 158E). Bonaldo (2000) proposed the distal thick sclerotization of the sperm duct as a synapomorphy of Corinninae, although his group has recently found that the structure occurs in most Castianeirinae as well (A. Bonaldo and D. Candiani, personal commun.); in this dataset it is found in *Castianeira trilineata* (fig. 158E). COMMENTS: *Corinna*: the AER from *C. ducke* (Bonaldo, 2000) (scored 1). *Falconina*: from Bonaldo (2000: fig. 101) (scored 1). *Paradiestus*: from Bonaldo (2000) (scored 1). *Phrurotimpus, Phrurolithus*: sperm duct with thick walls, thin before embolus, similarly illustrated in *P. difficilis* by Wiehle (1967: fig. 76) (scored 0). *Sesieutes*: with apical widened section, but not thickly sclerotized (fig. 161B) (scored 01). *Titanebo*: sperm duct markedly sinuous (scored 0).

347. Sperm duct sclerotization: 0. Sclerotized, thick wall, at least in basal section (fig. 153D). 1. Membranous, thin wall. In this dataset the only terminal with a membranous sperm duct is *Thaida* (Austrochilidae, personal obs.). The sperm duct has lost its sclerotized walls also in derived oonopids (Platnick et al., 2012).

348. Sperm duct spiral meander in ventral tegulum: 0. Absent (figs. 139C, 158E). 1. Present (fig. 159E). Corinnines have a meander of the sperm duct describing a regular spiral on the ventral side of tegulum (Platnick and Baptista, 1995; Bonaldo, 2000). COMMENTS: *Titanoeca*: complex, internal sperm duct (scored 0). *Clubiona*: similar as in corinnines, other species different, *C. maritima* fairly contorted (fig. 144B) (scored 01). *Orthobula*: there is a gland discharging close to embolus (scored 0). *Uliodon*: parts of sperm duct not touching tegulum walls, with voluminous tegular gland (scored 0). *Hispo*: sperm duct crosses internally through the tegulum (scored 0).

349. Embolus origin internal: 0. Exposed. 1. Internal to complex conductor (fig. 139D). See Griswold et al. (2005: char. 122). COMMENTS: *Titanoeca*: the embolus arises between tegulum and cymbium, and has a very complex associated conductor, but the base is exposed (scored 0). *Eilica*: the embolus has a long, sclerotized base arising internally in a tegular-embolar section (scored 0).

350. Separate embolic division: 0. Absent, embolus in one sclerotized piece (fig. 153A). 1. Present, a sclerotized basal section as a cylinder containing the sperm duct, separated from the embolus by a membranous articulation (fig. 155B). This embolic division includes the araneoid radix and the "distal sclerotized tube of apical division," which may be fully articulated as in *Dolomedes* (Sierwald, 1990). COMMENTS: *Xenoplectus*: I interpreted the articulated piece where the embolus arises as part of the tegulum, but at the base of embolus there is a further partial division (fig. 162D) (scored 01). *Camillina*: there is a separate basal division, but not containing the sperm duct (scored 0). *Eilica*: the embolar base is telescoped inside this section, not a complete cylinder (scored 0). *Gayenna*: the embolus base is partially divided by an incomplete membranous strip (fig. 156D, F) (scored 01).

351. Embolus attachment: 0. Fixed (figs. 144E, 153E, F). 1. Flexibly attached (figs. 139B, 145G, 148A, 153A). COMMENTS: *Thaida*: the subtegulum-tegulum is a continuous sclerotized band (scored 0). *Eriauchenius*: embolus base not exposed; Wood et al. (2012: fig. 9a) show dramatic distal expansion of the palpal bulb of *Eriauchenius*, exposing the embolus and other distal sclerites (scored ?). *Titanoeca*: complex, unclear (scored 1). *Metaltella*: not exposed, but arising from a membranous area (scored 1). *Calacadia, Desis*: internal, not exposed (scored ?). *Oxyopes*: fused to one of the two sclerotized remains of the tegulum (scored 0). *Trachelas mexicanus*: base of embolus with sclerotized rings (scored 01). *Phrurotimpus*: partially membranous areas surrounding embolar base (scored 01). *Eilica*: very large embolar base (scored 1). Cf. *Moreno* ARG: incomplete division (scored 01). *Lampona*: embolus arising from slightly unesclerotized area (scored 0). *Austrachelas*: anterior basal part is continuously sclerotized with tegulum (scored 01). *Tengella*: intermediate, weakly sclerotized articulation (scored 01). *Xenoctenus*: scored ambiguous, because the tegular distal division at embolar base might be an embolar projection instead (scored 01). *Philodromus*: with wide partial suture, although not movable (Huber, 1994) (scored 01). *Titanebo*: well-defined suture (scored 1). *Petrichus*: no suture at all (scored 0). *Heteropoda*: a meander in the sperm duct may indicate the place of fusion (scored 0). *Plexippus*: unsclerotized notch at embolus base (scored 01).

352. Embolar basal process: 0. Absent (figs. 140D, 145E). 1. Present. The base of embolus has a sclerotized process, continuous with the embolus (figs. 144A, 156E, 162D, 166D). COMMENTS: cf. Liocranidae LIB: a lamellar complex process (scored 1). *Camillina*: flat wide piece (scored 0). *Austrachelas*: ectal embolar process (!) (scored 1). *Platyoides*: a small process at the tip (scored 0). *Liocranoides*: complex embolus, some of the folds could be interpreted as processes (scored 01). *Raecius*: the sclerotized tegular process 2 (STP2) in Griswold (2002: fig. 51) (scored 1). *Odo bruchi*: a very long and thin process (scored 1).

353. Embolus prolateral furrow: 0. Absent. 1. Present. COMMENTS: *Filistata*: there is a short furrow (scored 01). *Thaida*, *Agroeca*, *Lauricius*: embolus very complex (scored 01). *Donuea*: thin furrow on complex embolus, unclear homology (scored 01). *Trachelas minor*, *Castianeira*, *Copa*: modified, screw shaped (scored 01). *Jacaena*: just a line (scored 0). *Camillina*: too modified (scored ?). *Eutichurus*: only apically (scored 01). *Liocranoides*: quite complex, but without furrow (scored 0). *Ciniflella* BRA: ventral-retrolateral furrow (scored 1).

354. Embolus screw shaped: 0. Absent, other shapes (fig. 158A). 1. Present. The embolus forms a tapering screw (figs. 158C, 159A, B, 163E), which usually corresponds to a complementary screw in the female copulatory openings (figs. 158G, 159C, 167D). COMMENTS: *Filistata*: very slightly so (scored 01). *Trachelas minor*: very slightly screw shaped, female copulatory opening also very slightly screwed (scored 01). *Trachelas mexicanus*: screw in the opposite direction compared to castianeirines, provisionally interpreted as homologous (scored 1). *Tibellus*: only the tip of the embolus forms a well-defined screw (fig. 36G) (scored 0).

355. Embolus tip wide, truncate, opening on thin transverse tube: 0. Absent. 1. Present (fig. 144D, F). COMMENTS: *Eriauchenius*: conformation too different (scored -). *Apostenus*: similarly as in *Liocranum*, a thin, short transverse ending of the sperm duct (scored 1). Cf. Liocranidae LIB: extensive, waving ribbon, but not tube (scored 0).

356. Median apophysis: 0. Present. The median apophysis typically is a hook-shaped, articulated sclerite, arising from the retrolateral side of the copulatory bulb (figs. 156A, G, 166B). 1. Absent (figs. 159A, 164A, 166A). COMMENTS: *Hypochilus*: the structure labeled "MA?" in Coddington (1990: fig. 9) is the base of the embolus, and continues spiraling on the other side (scored 1). *Thaida*: the thin piece previously identified as embolus in Forster et al. (1987) here interpreted as in Griswold et al. (2005) (scored 0). *Eresus*, *Megadictyna*, *Macrobunus*: interpreted as in Griswold et al. (2005) (scored 1). *Oecobius*: the articulated sclerite (scored 0). *Uloborus*: interpreted as in Coddington (1990) and Griswold et al. (2005) (scored 0). *Eriauchenius*: interpreted as in Griswold et al. (2005) (scored 0). *Nicodamus*: interpreted as in Harvey (1995), apically membranous, may be a conductor instead, but there are other apophyses related to the embolus (scored 0). *Psechrus*: present in *Fecenia* (scored 1). *Cyrioctea*: median apophysis conductor-shaped, with small basal branch (scored 0). *Pseudoctenus*: median apophysis as a sclerotized hook plus posteriorly directed fleshy lobe (scored 0). *Corinna*: the *Corinna* tegular process (PTC) of Bonaldo (2000) may be interpreted as a median apophysis, but it is prolateral to the conductor (scored 01). *Hortipes*: interpreted as in Bosselaers and Jocqué (2000) (scored 0). Cf. Liocranidae LIB: two sclerotized articulate sclerites, the one closer to embolus base interpreted as a conductor (scored 0). *Jacaena*, *Sesieutes*: tentatively identified as the small whitish prolongation besides the conductor tip (scored 0). *Oedignatha*: tegular sclerite identified as median apophysis, but might be identified as a conductor instead (fig. 161G, H) (scored 0). *Trachycosmus*: two sclerites, one identified as the median apophysis, the other as the conductor (scored 1). *Fissarena*: both conductor and median apophysis guide the embolus (scored 0). *Desognaphosa*: Just a fleshy lobe. Homology different from Platnick (2002); the large sclerite leading the embolus arises just from the base of embolus, has granulose basal texture, and has a large canal to receive the embolus, it is identified as conductor (scored 1). *Cithaeron*: interpretation as in Platnick (1991), the median apophysis looks like a hyaline conductor (scored 0). *Macerio*: median apophysis stick-shaped (scored 0). *Strotarchus*: there is only a central sclerite, part of the embolic division (scored 1). *Uliodon*: present but vestigial (scored 0). *Philodromus*: with "no apparent function during copulation" (Huber, 1995a: 156) (scored 0). *Petrichus*: no vestige of median apophysis found with SEM (scored 1). *Stephanopis ditissima*: just a vestige (scored 0). *Hispo*: not a subtegular apophysis (see Szüts and Scharff, 2009) (scored 1).

357. Median apophysis articulation: 0. Flexibly attached. The median apophysis connects with the tegulum via an area of soft cuticle (fig. 156A). 1. Fixed insertion. In this dataset, a fixed median apophysis occurs only in outgroups and in cases where the fusion is obviously a sclerotized articulation (fig. 147C). COMMENTS: *Mimetus*: continuous with conductor (scored 0). *Aglaoctenus*: the median apophysis arises from a partially sclerotized area (scored 01). *Miturga* cf. *lineata*: two sclerites arising at the base of the embolus, the median apophysis identified as the more conservative, usually hook shaped, as in Miturgidae QLD, *Zora*, *Teminius*, and other Miturgidae (see next character) (scored 0). *Lauricius*: partially fused (scored 01). *Philodromus*: small, more prominent in *C. californicus* (scored 0). *Hovops*: at embolus base, on top of a turret! (scored 0). *Anyphops*: placed on a long membranous tube (fig. 154B) (scored 0).

358. Median apophysis continuous with embolus base, directed forward: 0. Absent, other conformations (figs. 148A, E, 150A). 1. At embolic base, directed forward (miturgid conformation). The median apophysis is continuous with the base of the embolus (figs. 145G, 146A, D). This character state represents a palpal conformation characteristic of miturgids. COMMENTS: *Donuea*, *Liocranoides*, *Cocalodes*: unclear but compatible (scored 01). *Miturga gilva*: there may be a further synapomorphy with *Miturga* cf. *lineata* in the pointed anterior projection of the median apophysis (fig. 146C) (scored 1).

359. Conductor: 0. Present (figs. 148A, 154C, 159G, 162A, C). The conductor is typically a semimembranous sclerite, which may be partially or totally sclerotized or hyaline, often with a canal or depression fitting part of the embolus (hence its name). 1. Absent (figs. 163E, 166E). The homology of the conductor is always contentious in spiders. In this study the conductor was identified as a tegular sclerite or membranous outgrowth, somehow associated with the embolus (e.g., with a matching canal, holding the embolus tip), and in the prolateral-ventral-apical region of the copulatory bulb; the median apophysis is much more conservative, usually in the retrolateral region. One of the main issues is the simultaneous occurrence of two structures, each of which might arguably be scored as a conductor (e.g., a "membranous tegular process" and a "hyaline conductor," as in Griswold, 1993: chars. 8 and 22). Not surprisingly, this character is among the most homoplasious in the dataset, and the implied weighting makes it uninfluential in the analysis (inactivating chars. 359–361 produces the same trees, except for the placement of *Lyssomanes* sister to *Plexippus* + *Hispo*). COMMENTS: *Megadictyna*: interpreted as in Griswold et al. (2005) (scored 0). *Titanoeca*: long tegular groove, but also a closed loop protecting the embolus (scored 0). *Metaltella*, *Calacadia*, *Desis*: the embolar cover, interpreted as in Griswold et al. (2005) (scored 0). *Aglaoctenus*: I identified the hook leading the embolus as a part of the conductor, as in Santos and Brescovit (2001) and Santos et al. (2003: LAC, "lateral apophysis of conductor"), but see Sierwald (2000), who reports many apophyses in *Sossipus*, not evident which one may be a conductor (scored 0). *Clubiona*: the fleshy apical lobe (scored 0). *Trachelopachys*: a membranous structure close to the embolus base, similar to the membranous tegular process in other terminals (e.g., *Zoropsis*) (scored 0). *Brachyphaea*: Perhaps fused to tegulum, because there is a suture at embolus base. Coded as a tegular furrow as in *Paccius* (but in *Paccius* the furrow is prolonged in a membraneous structure) (scored 1). *Phrurolithus*, *Phrurotimpus*: a membranous lobe at embolus base may be a relict of conductor, may be a synapomorphy (figs. 164E, 165C) (scored 1). *Teutamus*: fused to the tegulum, can be tentatively identified because of the similarity with *Sesieutes* (scored 0). *Jacaena*: tentatively identified as the sclerite leading the embolus, fused to the tegulum (see comments on median apophysis), it can be identified because of the similarity with *Sesieutes*; there may be an additional character to unite *Sesieutes*, *Jacaena* and *Teutamus* in this conformation (figs. 160A, B, 161A–D) (scored 0). *Oedignatha*: here interpreted as reduced (the apical projecting border of the tegulum, more projecting in *O. scrobiculata*) (scored 1). *Prodidomus*: there are membranous folds at embulus base (scored 1). *Doliomalus*: only a membranous window at the side of an extension of the tegulum (scored 01). *Gayenna*: the "C2" of Ramírez (2003), reinterpreted according to Ramírez (2007) (scored 0). *Systaria*: labeled as median apophysis by Deeleman-Reinhold (2001) (scored 0). *Philodromus*: Perhaps sclerotized but translucent, membranous according to Huber (1995b: 156): "Rotation [of the copulatory bulb] is apparently stopped by the membranous "conductor" that finally becomes arrested by contact with the ventral tibial apophysis. It is unclear whether this "conductor" also assists the introduction of the embolus into the insemination duct") (scored 1). *Petrichus*: only a membranous apical area with a furrow where the embolus fits (scored 01). *Titanebo*: only a membranous apical area with a furrow (scored 01). *Eusparassus*: just a membranous apical part of the tegulum (scored 0). *Aphantochilus*: a sclerotized apical lamella totally fused with the tegulum (scored 0).

360. Conductor sclerotization: 0. Sclerotized (fig. 147D). 1. Hyaline (fig. 142B) or membranous (figs. 145C, E, F, 154F). COMMENTS: *Homalonychus*: completely sclerotized but with the same shape (apical fan) as in many hyaline conductors (scored 0). *Vulsor*: basal portion membranous, median hyaline, apical sclerotized (scored 01). *Pronophaea*: sclerotized process with basal hyaline conductor (scored 01). *Olbus, Pseudocorinna*: heterogeneous, complex (scored 01). *Xenoplectus*: very evident tube in an expanded bulb, hidden in SEM images (scored 1). Cf. Gnaphosoidea TEX: apparently two conductors, one sclerotized, the other membranous (scored ?). *Lampona, Lamponella*: membranous (scored 1). *Anyphaena*: both membranous and sclerotized parts (scored 01). *Zora*: hyaline, but base sclerotized, articulated (scored 1). *Zorocrates*: the tegular apophysis (Griswold et al., 2005: fig. 186B) looks like an extra sclerotized conductor (may be part of the embolar division instead) (scored 1). *Philodromus*: sclerotized but translucent (scored 0). *Tibellus*: intermediate (scored 01). *Anyphops*: sclerotized tegular furrow ending in translucent conductor (scored 01). *Heteropoda*: intermediate (scored 01).

361. Sclerotized conductor articulation: 0. Fixed insertion (fig. 152B). 1. Articulate (figs. 151D, 155C). This character was considered not applicable when the conductor is totally membranous. COMMENTS: *Metaltella*: extensively fused to tegulum (scored 0). *Meedo*: all central tegular area membranous (scored 01). *Anyphops*: unclear, *A. barbertonensis* seemingly separated by unsclerotized areas (scored 01). *Tibellus*: intermediate (scored 01).

362. Other tegular articulate sclerites (in addition to the conductor and the median apophysis): 0. None. 1. At base of conductor. 2. At base of embolus (figs. 154D, 157F). 3. At base of median apophysis. Some miturgines have a spine-shaped sclerite parallel to the median apophysis (fig. 145B; Raven and Stumkat, 2003: fig. 5). The sclerite was also found in the diaprograptine *Diaprograpta* (Raven, 2009, as "accessory spine"). COMMENTS: *Titanoeca*: a piece at the base of embolus is interpreted as an embolar process (scored 0). *Metaltella*: the anterior hook is the embolar base (scored 0). *Calacadia*: there is an apical sclerotized hook, not clear whether it is a separate sclerite; it seems deeply connected with the tegular base (scored 012). *Desis*: the fleshy finger, not clear at base of what (scored 012). *Macrobunus*: a small sclerite, tegular apophysis (TA) in Griswold et al. (2005: fig. 193B) (scored 3). *Cyrioctea*: a large central swelling in *C. spinifera*, smaller in *C. calderoni*, absent in *C. aschaensis* (scored 02). *Zoropsis*, *Uliodon*: a hyaline flap, not a sclerite, that would have been coded as conductor if the apical one was absent (fig. 142B; membranous tegular process (MTP) in Boesselaers, 2002: fig. 1C) (scored 0). *Oxyopes*: sclerotized relics of the tegulum fused to the conductor medially and dorsally (scored 0). *Aglaoctenus*: there is a projection at the base of the conductor interpreted as part of the conductor (lateral apophysis of conductor, Santos and Brescovit, 2001) (scored 0). *Corinna*: the *Corinna* tegular process (PTC) of Bonaldo (2000) may be interpreted as a median apophysis or as a further sclerite (scored 01). *Pronophaea*: a flat tegular process (scored 2). *Procopius*: two apophyses at sides of conductor (scored 0). *Phrurolithus*: retrolateral apical tegular projection also found in *Otacilia* (scored 0). *Camillina*: the embolus comes from a more or less demarcated tegular section (scored 2). Cf. Gnaphosoidea TEX: it depends on the interpretation of the conductors (scored ?). *Lamponella*: two sclerotized cusps may come from one or two separate sclerites, at base of embolus and conductor, all close together (scored 12). *Platyoides*: a small projection of the tegulum at the base of embolus (scored 0). *Anyphaena*: secondary conductor in Ramírez (2007) (scored 2). *Gayenna*, *Amaurobioides*: the paramedian apophysis (Ramírez, 2003, 2007) (scored 1). *Miturga gilva*: very small (scored 3). *Syspira*: there may be a translucent extension parallel to the median apophysis, apparently variable within the same species, not scored as a sclerite (scored 0). *Xenoctenus*: the central sclerite found in *Odo patricius* is more fused, but still some weakly sclerotized separations remain; this reinforces the distinction of this piece with the miturgid median apophysis (scored 02). *Zorocrates*: the tegular apophysis (Griswold et al., 2005: fig. 186B). *Heteropoda*: There is an apical dorsal tegular projection similar to a conductor, hidden in the unexpanded bulb. This might instead be the conductor, and the large articulated conductor might be the median apophysis (scored 0). Sparianthinae VEN: bulbous area, similar to the conductor in Amaurobioidinae (scored 2).

FEMALE GENITALIA

The female ovaries connect to the epigastric fold via the oviduct. The uterus externus is the last section of the oviduct, and is the only part of the oviduct lined by cuticle (figs. 99A, 167F, 168A). The uterus externus ends in the gonopore, usually hidden inside the epigastric furrow (fig. 169A). Female spiders store the sperm in receptacles called spermathecae, hence, the fertilization does not occur during mating. In basal spiders the flow of sperm is bidirectional, as the same duct is used to insert the sperm during mating, and to draw sperm for fertilization; this is called a haplogyne system. Females with haplogyne genitalia have the copulatory opening inside the epigastric furrow, often arising from a bursa copulatrix (fig. 168B), and the epigastrium lacks complex sclerotizations (fig. 167A). In Entelegynae the sperm flow is unidirectional; the sperm is inserted through a copulatory duct, and drawn from the spermatheca through a fertilization duct (figs. 168C, D, 169C). Females with entelegyne genitalia have the copulatory openings exposed, associated with an external sclerotized structure, the epigyne (fig. 167B).

EPIGYNE: The sclerotized epigyne of entelegyne spiders is generally composed of three plates: the median field and two lateral lobes (fig. 167E). The limits between those plates are marked by the epigynal folds, usually ending in or near the copulatory openings. During the ontogeny of the epigyne, a precursor of the epigynal fold invaginates to form the complete duct system: copulatory duct–spermatheca–fertilization duct (Sierwald, 1989). Externally, the fold may remain well demarcated (fig. 167E), as a superficial suture (fig. 167C), or not evident at all (fig. 167D). While the fertilization duct remains united to the external cuticle by the invaginated fold, the copulatory duct may retain a connection (fig. 168C) or be entirely separated from the external cuticle (fig. 168E). The epigyne may have small gland ducts discharging through pores (fig. 169C, E). These epigynal cuticular glands may be placed on the proximal copulatory ducts (fig. 168D), as well as on the posterior wall of the epigastric fold (fig. 169A). Some male spiders produce a mating plug to block the copulatory openings after mating (figs. 167E, 169E).

SPERMATHECAE: The receptacles for sperm storage are generically referred to as spermathecae. While in haplogyne spiders the spermathecae are typically blind sacks connected to a duct or stalk (fig. 168A, B), in entelegynes at least one spermatheca on each side connects to both the copulatory and the fertilization ducts. Entelegynes usually have two pairs of ball-shaped receptacles, the primary and secondary spermathecae.

PRIMARY SPERMATHECA: The receptacle connecting to the fertilization duct is here called *primary spermatheca* (= "base of spermatheca," Sierwald, 1989; "spermatheca" in most usages) (figs. 168C–E, 169A–C). The primary spermatheca and the copulatory ducts are covered by small glandular pores, smaller than those of the secondary spermatheca, without noticeable cuticular ducts (fig. 169A, B). On the primary spermatheca there may be a defined patch of larger gland pores, here called Bennett's gland (= "dictynoid" pore, Bennett, 1992) (figs. 168D, 169D). In some groups Bennett's gland may be shaped as an everted lobe (fig. 168E).

SECONDARY SPERMATHECA: The blind ending receptacle with large glandular pores and ducts is here called *secondary spermatheca* (= "head of spermatheca," Sierwald, 1989; "accessory bulb" of Carico and Holt, 1964, and Ramírez, 2003) (figs. 168C–E, 169A–C). The gland ducts are similar to those found on spermathecae and ducts of many haplogyne Araneomorphae (fig. 168B) and Mygalomorphae (Michalik et al., 2005). The secondary spermatheca is usually smaller than the primary, but in some groups they may be of similar size (fig. 168E), or the secondary spermatheca may even be the only significant receptacle (fig. 169A). The secondary spermatheca is usually connected to the copulatory duct by its own duct (fig. 168C), but the latter duct may be very short (fig. 168D), or the secondary spermatheca may be reduced to a patch of gland

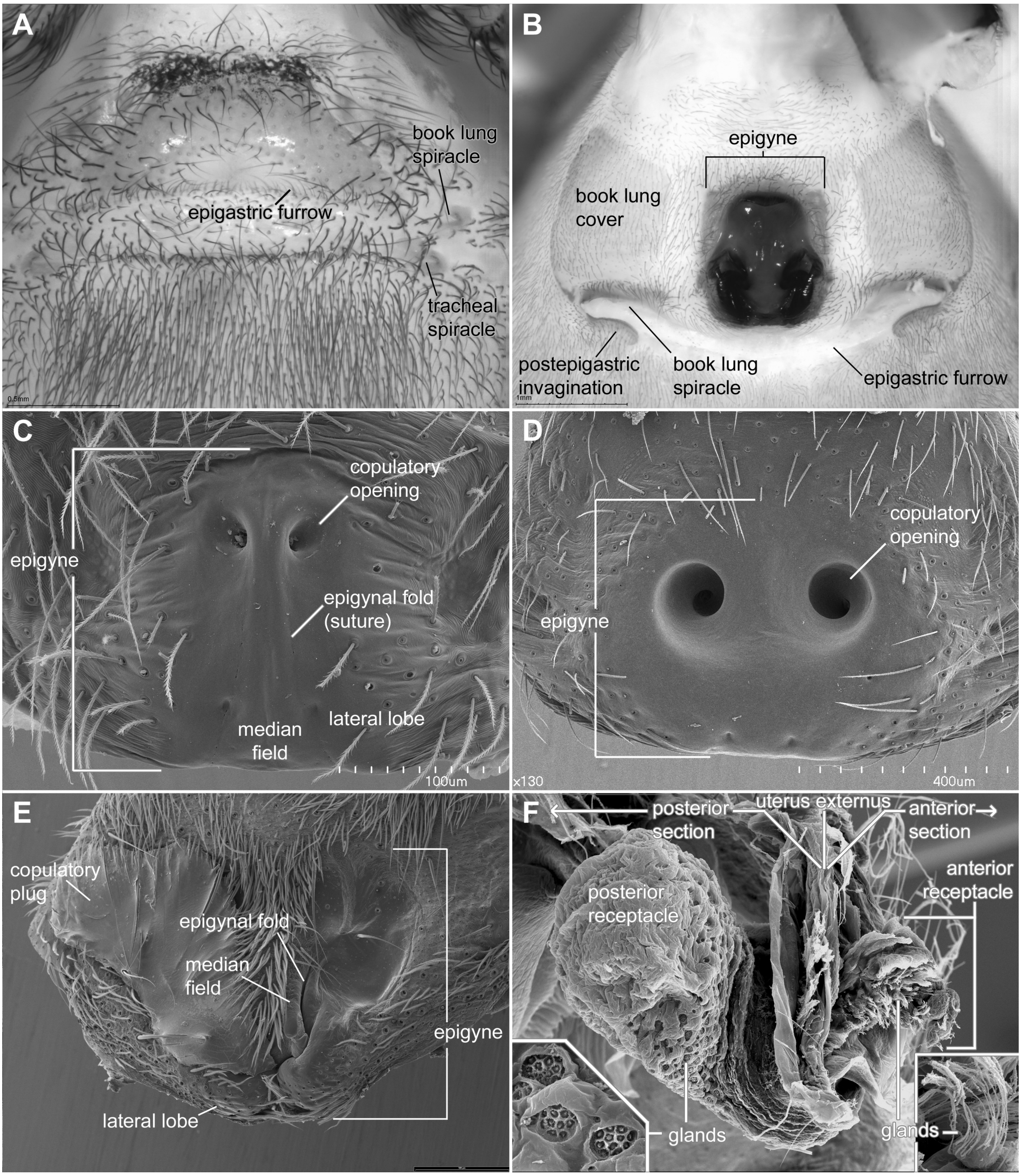

A
book lung spiracle
epigastric furrow
tracheal spiracle
0.5mm
B
epigyne
book lung cover
postepigastric invagination
book lung spiracle
epigastric furrow
1mm
C
copulatory opening
epigyne
epigynal fold (suture)
median field
lateral lobe
100um
D
copulatory opening
epigyne
x130
400um
E
copulatory plug
epigynal fold
median field
epigyne
lateral lobe
F
posterior section
uterus externus
anterior section
anterior receptacle
posterior receptacle
glands
glands

Fig. 167. Structures of female genitalia. **A.** *Ariadna boesenbergi* (Segestriidae) ventral. **B.** *Austrachelas pondoensis* (Gallieniellidae) ventral. **C.** *Trachelas minor* (Trachelidae) ventral. **D.** *Trachelas mexicanus* (Trachelidae) ventral. **E.** *Uliodon* cf. *frenatus* (Zoropsidae) ventral. **F.** *Segestria florentina* (Segestriidae) digested, dorsal-lateral.

pores on the copulatory duct or the primary spermatheca (fig. 169B, C).

COPULATORY DUCT: The copulatory opening receives the embolus of the male copulatory bulb. The copulatory duct is usually correlated in shape and length with the embolus. The first segment of the copulatory duct is often flexible, not sclerotized (fig. 169D).

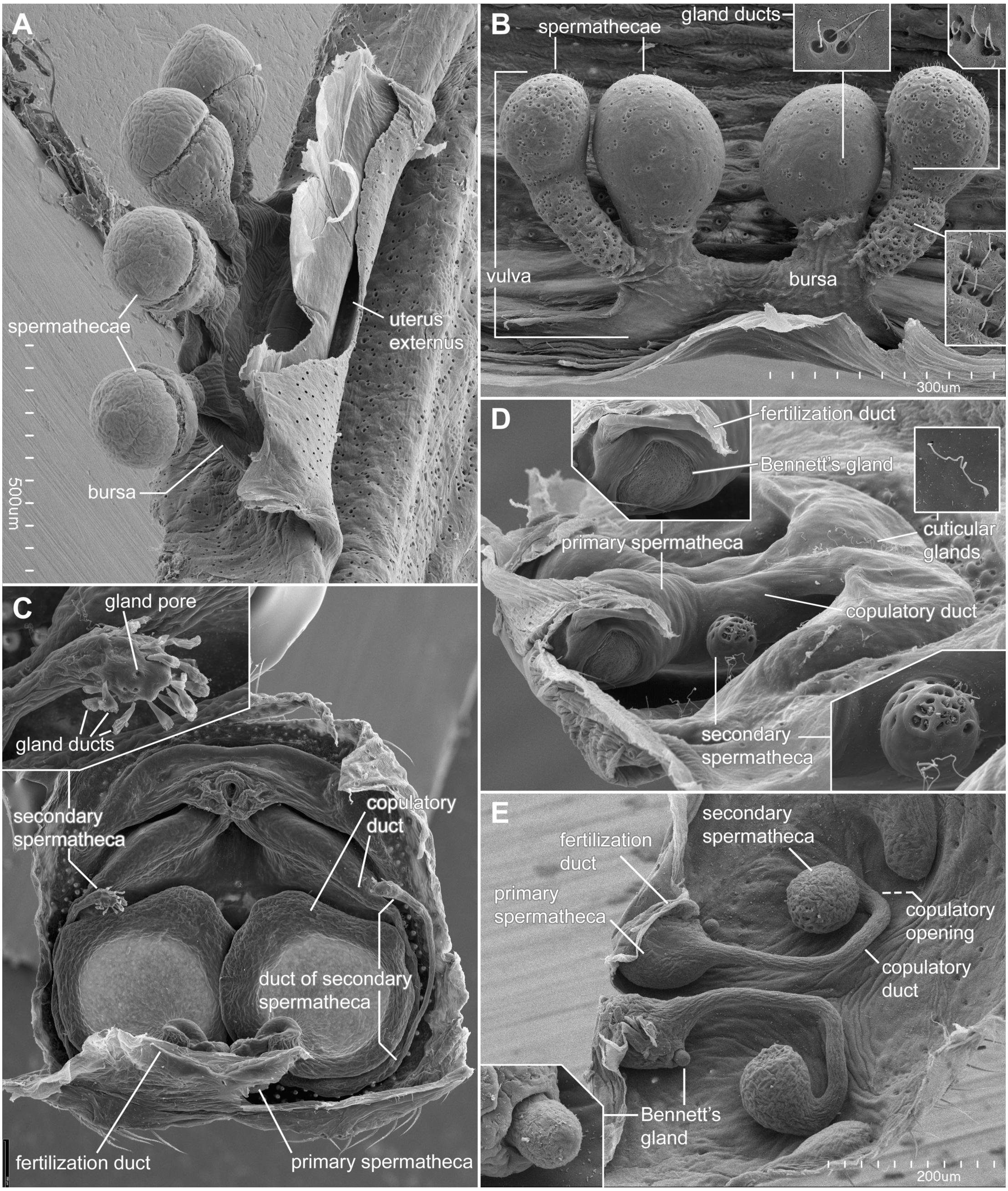

A
spermathecae
uterus externus
bursa
500um
B
spermathecae
gland ducts
vulva
bursa
300um
C
gland pore
gland ducts
secondary spermatheca
copulatory duct
duct of secondary spermatheca
fertilization duct
primary spermatheca
D
fertilization duct
Bennett's gland
primary spermatheca
cuticular glands
copulatory duct
secondary spermatheca
E
secondary spermatheca
fertilization duct
primary spermatheca
copulatory opening
copulatory duct
Bennett's gland
200um

Fig. 168. Structures of female internal genitalia, digested. **A.** *Antrodiaetus robustus* (Antrodiaetidae). **B.** *Hypochilus pococki* (Hypochilidae). **C.** *Doliomalus cimicoides* (Trochanteriidae). **D.** *Xiruana gracilipes* (Anyphaenidae). **E.** *Legendrena perinet* (Gallieniellidae).

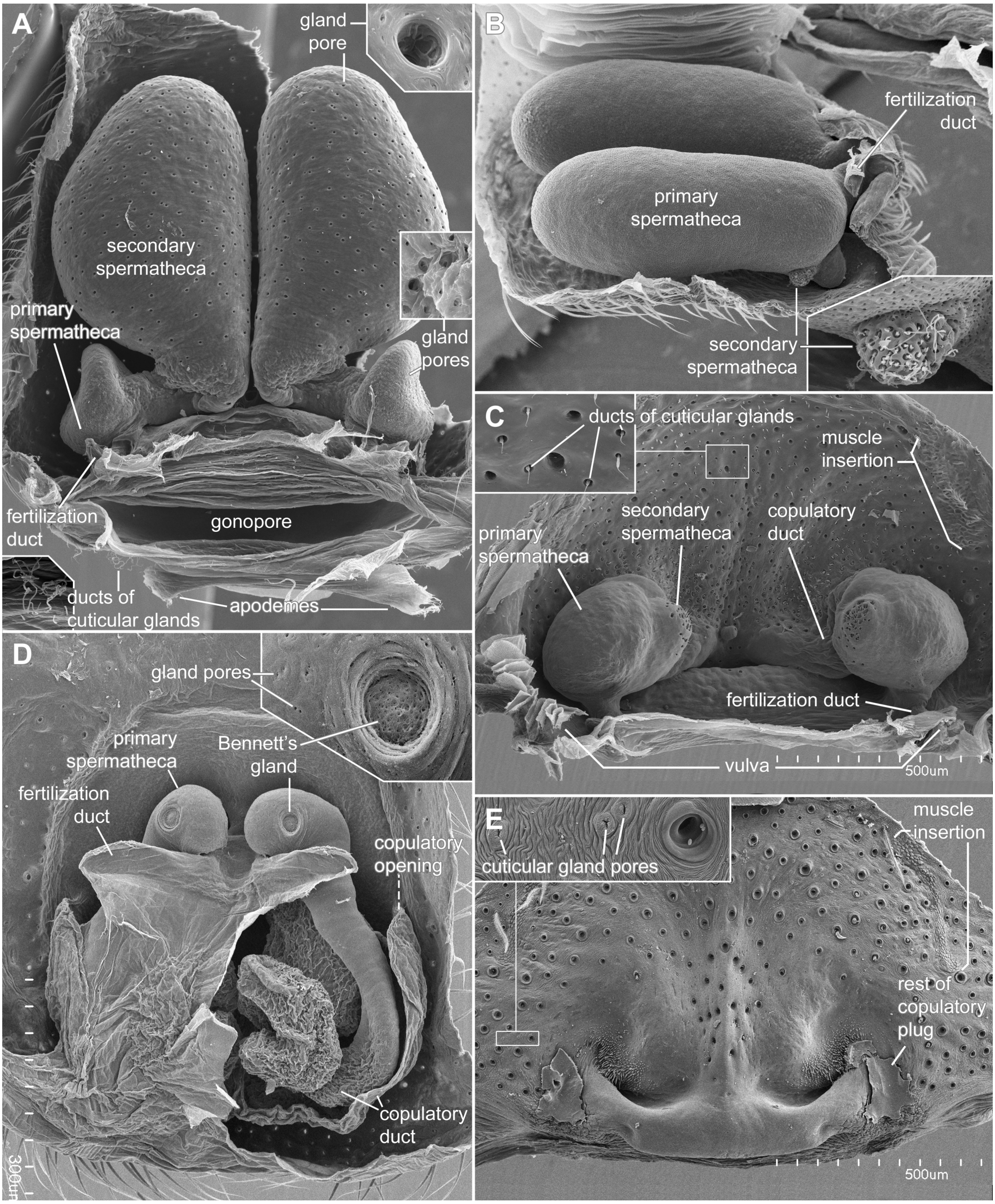

A
gland pore
secondary spermatheca
primary spermatheca
gland pores
fertilization duct
gonopore
ducts of cuticular glands
apodemes
B
fertilization duct
primary spermatheca
secondary spermatheca
C
ducts of cuticular glands
muscle insertion
secondary spermatheca
copulatory duct
primary spermatheca
fertilization duct
vulva
500um
D
gland pores
primary spermatheca
Bennett's gland
fertilization duct
copulatory opening
copulatory duct
300um
E
cuticular gland pores
muscle insertion
rest of copulatory plug
500um

Fig. 169. Structures of female genitalia, digested. **A.** *Paradiestus penicillatus* (Corinnidae). **B.** *Spartaeus wildtrackii* (Salticidae). **C.** *Cycloctenus nelsonensis* (Cycloctenidae) dorsal. **D.** *Trachycosmus sculptilis* (Trochanteriidae). **E.** *Cycloctenus nelsonensis* (Cycloctenidae), ventral.

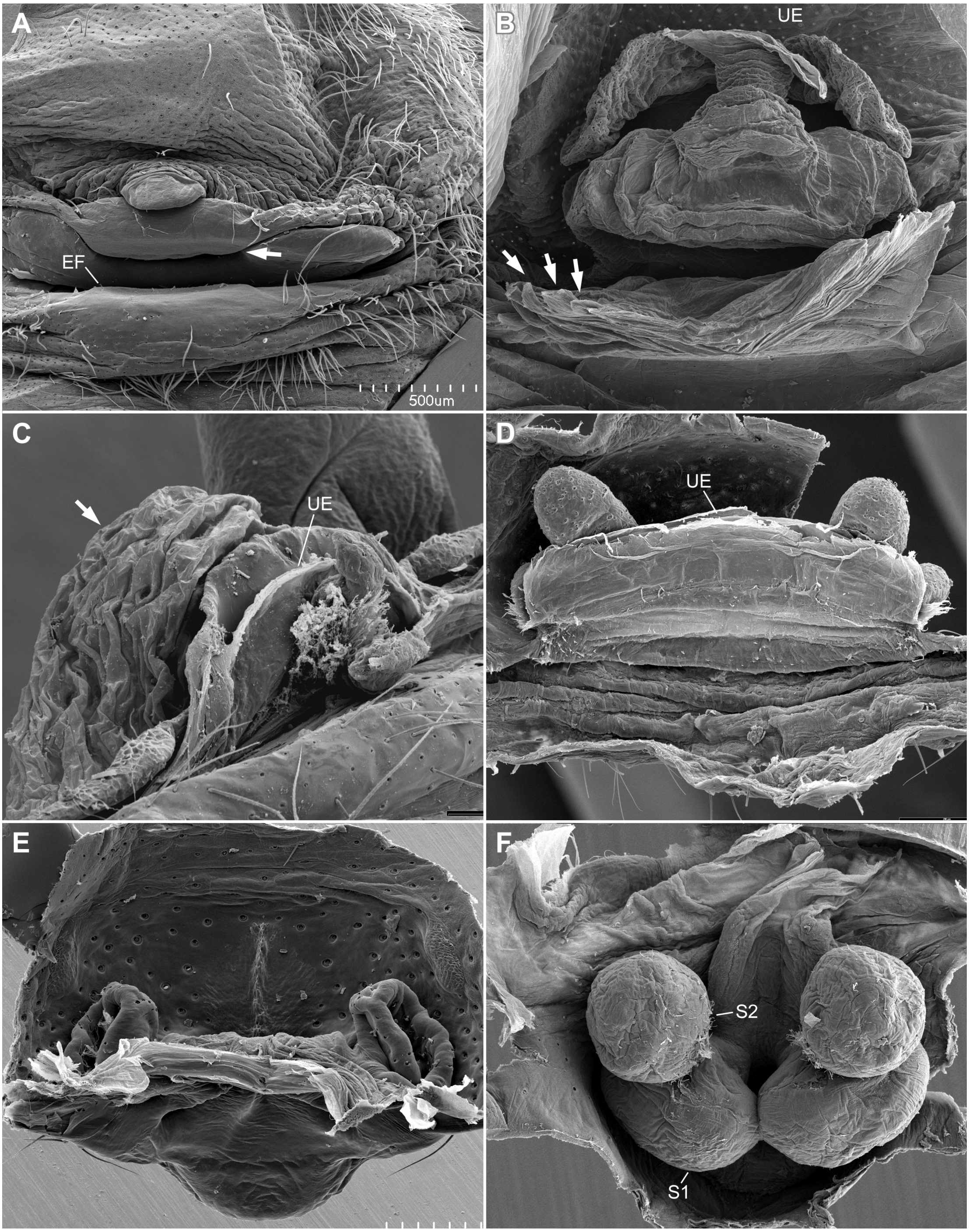


Fig. 170. Female genitalia, digested. **A.** *Thaida peculiaris* (Austrochilidae) ventral, arrow to gonopore fold. **B.** Same, dorsal, arrows to muscle attachments. **C.** *Ariadna mollis* (Segestriidae) dorsal anterior lateral, arrow to posterior receptacle. **D.** *Stedocys leopoldi* (Scytodidae) dorsal. **E.** *Nicodamus mainae* (Nicodamidae) dorsal. **F.** *Mimetus hesperus* (Mimetidae) dorsal.

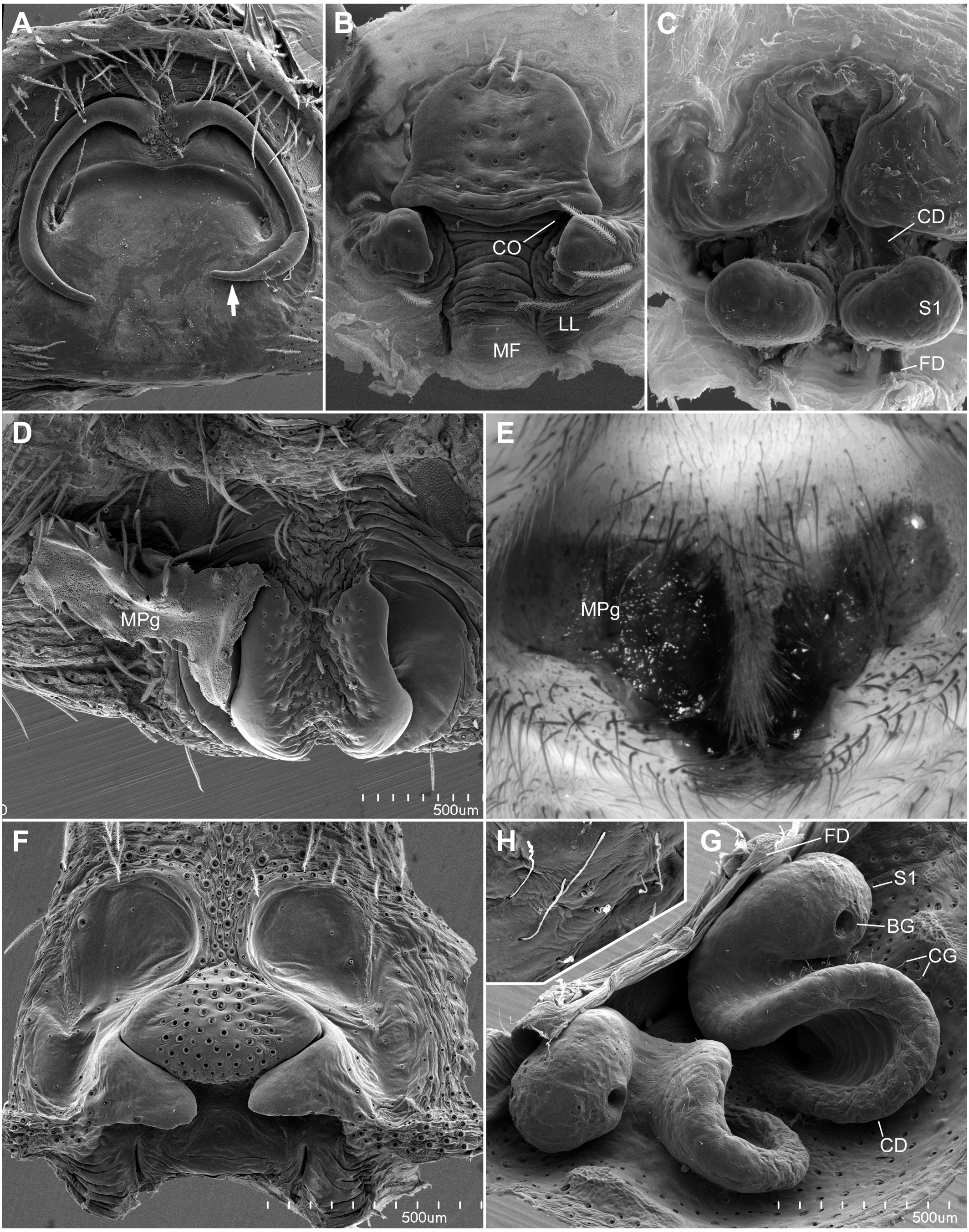

A
B
CO
LL
MF
C
CD
S1
FD
D
MPg
500um
E
MPg
F
500um
H
G
FD
S1
BG
CG
CD
500um

Fig. 171. Structures of female genitalia. **A.** *Metaltella* sp. (Amphinectidae) ventral, arrow to epigynal teeth. **B.** *Ciniflella* BRA (Tengellidae) ventral. **C.** Same, dorsal. **D.** *Tengella radiata* (Tengellidae) ventral, showing copulatory plug (removed from left side). **E.** *Uliodon* cf. *frenatus* (Zoropsidae) ventral, showing copulatory plug. **F.** *Homalonychus theologus* (Homalonychidae) ventral. **G.** *Cybaeodamus taim* (Zodariidae) dorsal anterior. **H.** Same, detail of ducts of cuticular glands on copulatory ducts.

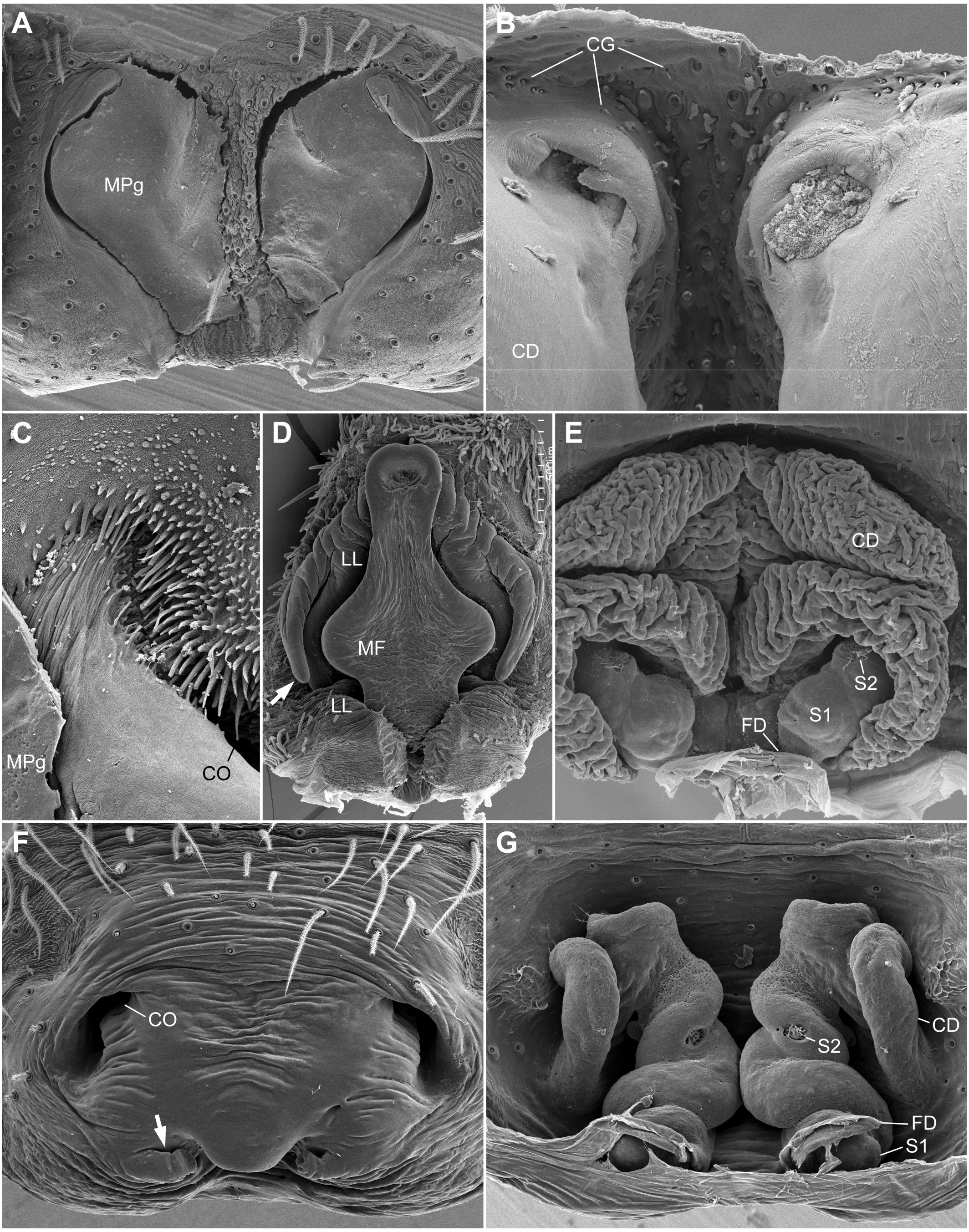


Fig. 172. Structures of female genitalia. **A.** *Toxopsiella minuta* (Cycloctenidae) ventral, showing massive copulatory plugs. **B.** Same, dorsal, detail of anterior portion of spermathecae showing cuticular gland ducts. **C.** *Cycloctenus nelsonensis* (Cycloctenidae) ventral, detail of epigyne with copulatory plug partially removed. **D.** *Borboropactus bituberculatus* (Thomisidae) ventral, arrow to epigynal teeth. **E.** *Stephanopis ditissima* (Thomisidae) dorsal. **F.** *Geraesta hirta* (Thomisidae) ventral, arrow to epigynal teeth. **G.** Same, dorsal.

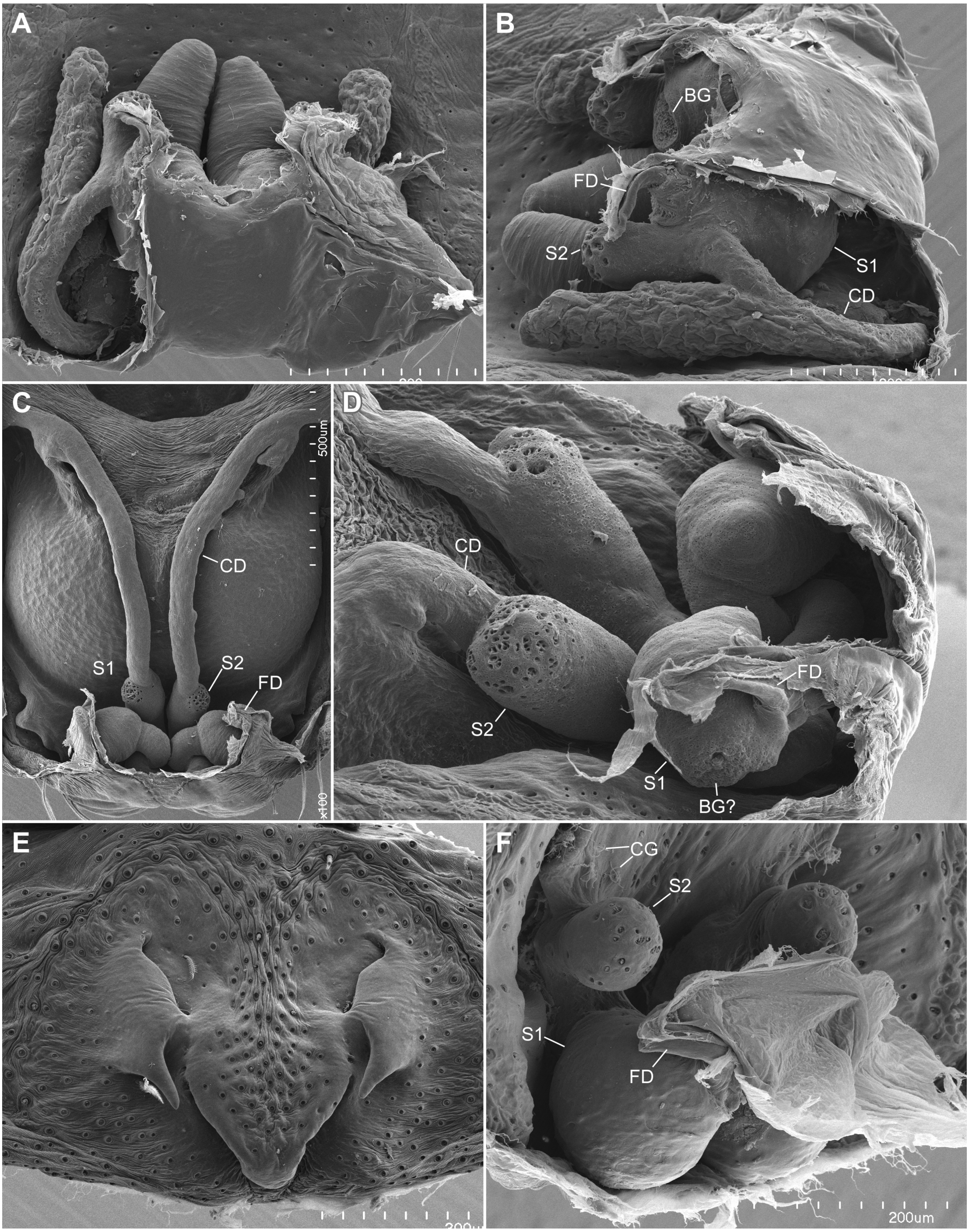

A
B
BG
FD
S2
S1
CD
C
500um
CD
S1
S2
FD
x100
D
CD
FD
S2
S1
BG?
E
F
CG
S2
S1
FD
200um

Fig. 173. Structures of female genitalia, Clubionidae and *Neoanagraphis*. **A.** *Clubiona pallidula*, ventral. **B.** Same, dorsal lateral. **C.** *Elaver* cf. *tigrinella* from Mexico, Hidalgo, Jacala, dorsal. **D.** *Elaver* cf. *tigrinella* from Costa Rica, Monteverde, Puntarenas, dorsal lateral. **E.** *Neoanagraphis chamberlini*, ventral. **F.** Same, dorsal lateral.

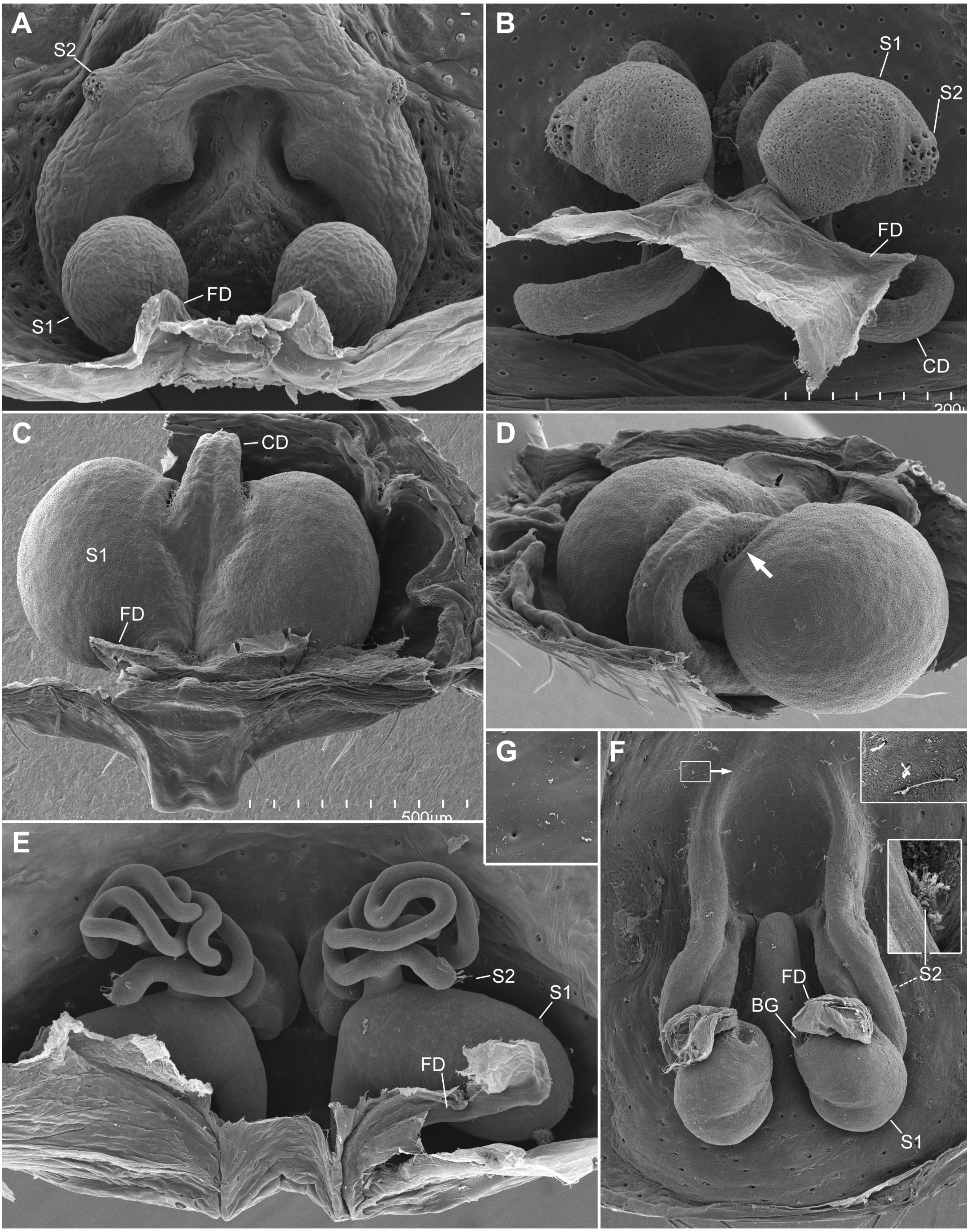

A
S2
FD
S1
B
S1
S2
FD
CD
200µ
C
CD
S1
FD
500µm
D
G
F
FD
BG
S2
S1
E
S2
S1
FD

Fig. 174. Structures of female genitalia, *Philodromus aureolus* (Philodromidae) and Salticidae. **A.** *Philodromus aureolus*, dorsal. **B.** *Cocalodes longicornis*, dorsal, cuticle partially removed. **C.** *Portia schultzi*, dorsal, epigyne partially removed. **D.** Same, lateral anterior, arrow to patch of pores. **E.** *Lyssomanes viridis*, dorsal. **F.** *Plexippus paykulli*, dorsal, cuticule removed, inset to cuticular gland ducts and to secondary spermatheca. **G.** Same, gland outlets on epigyne, ventral.

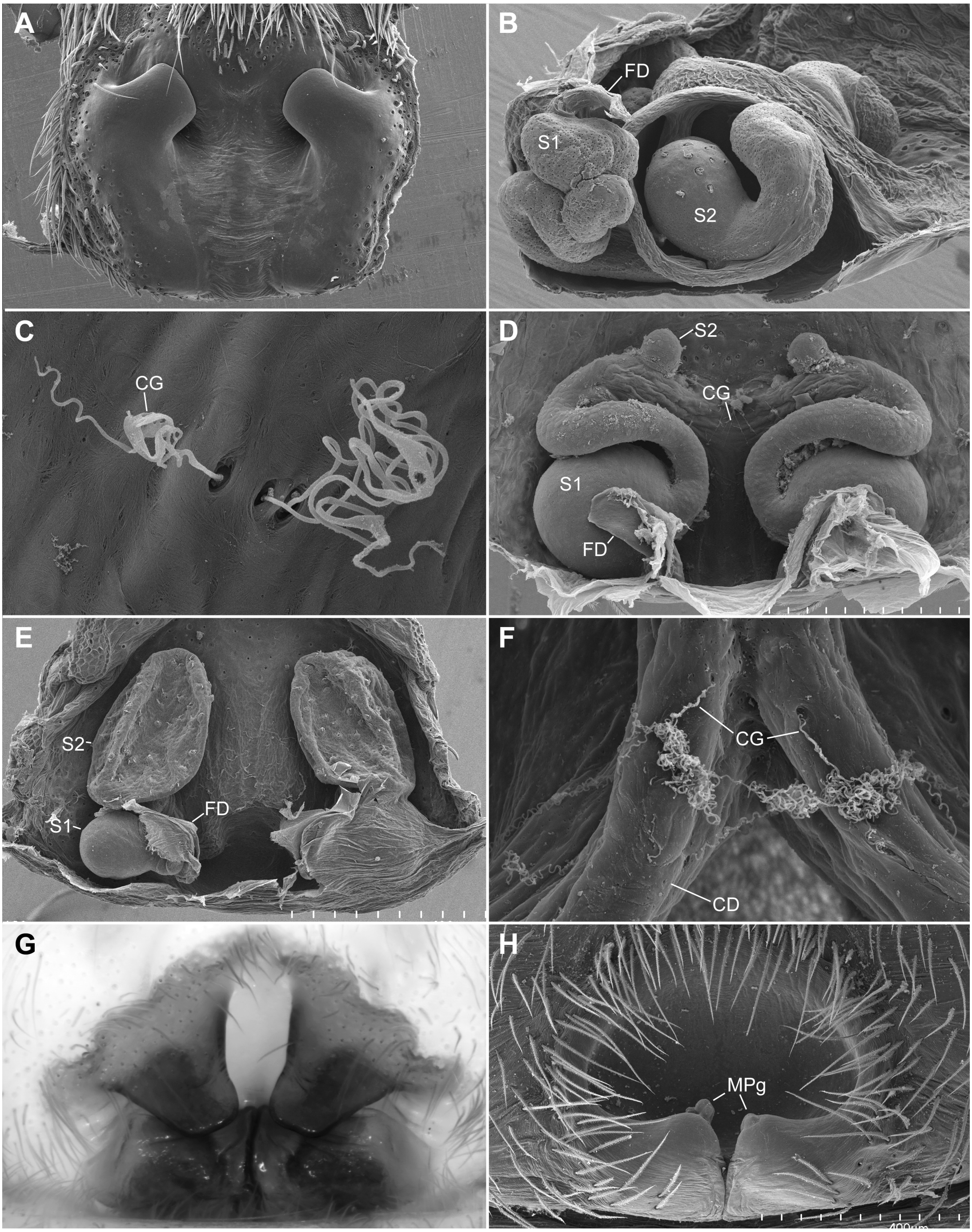


Fig. 175. Structures of female genitalia. **A.** *Mituliodon tarantulinus* (Miturgidae) ventral. **B.** *Syspira eclectica* (Miturgidae) lateral, epigyne cuticle removed. **C.** *Miturga* cf. *lineata* (Miturgidae) ducts of cuticular glands, dorsal. **D.** *Zora spinimana* (Miturgidae) dorsal. **E.** *Systaria* sp. (Miturgidae) female. **F.** *Paravulsor* sp. (Miturgidae) ducts of cuticular glands, dorsal. **G.** *Eutichurus lizeri* (Eutichuridae) ventral. **H.** *Macerio flavus* (Eutichuridae) ventral.

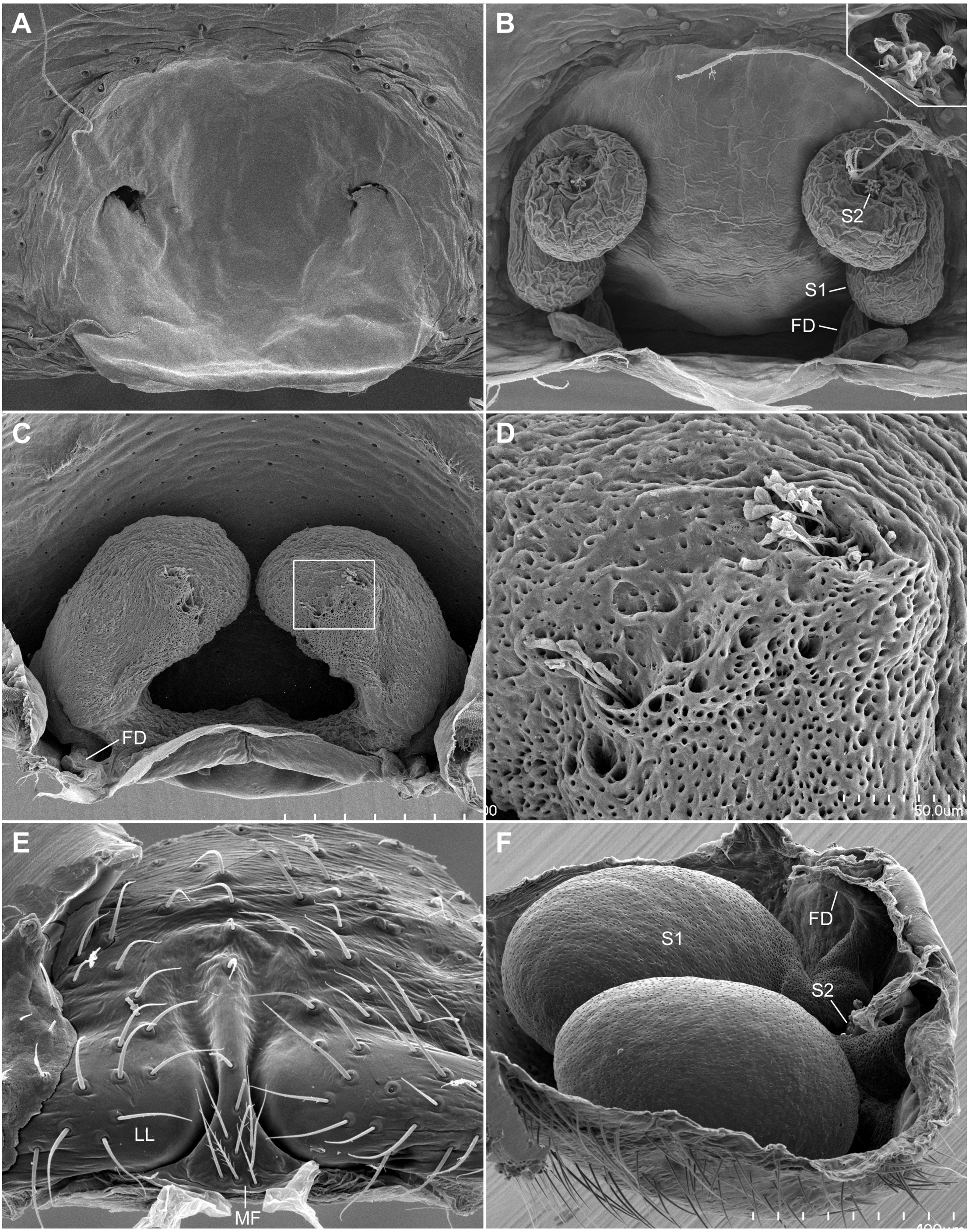


Fig. 176. Structures of female genitalia. **A.** *Malenella nana* (Anyphaenidae) ventral. **B.** Same, inset to left secondary spermatheca. **C.** *Procopius* cf. *aetiops* (Corinnidae) dorsal, inset on S2 area, detail in D. **D.** Same, inset to right secondary spermatheca. **E.** *Pronophaea proxima* (Corinnidae) ventral. **F.** *Brachyphaea* cf. *simoni* (Corinnidae) dorsal lateral.

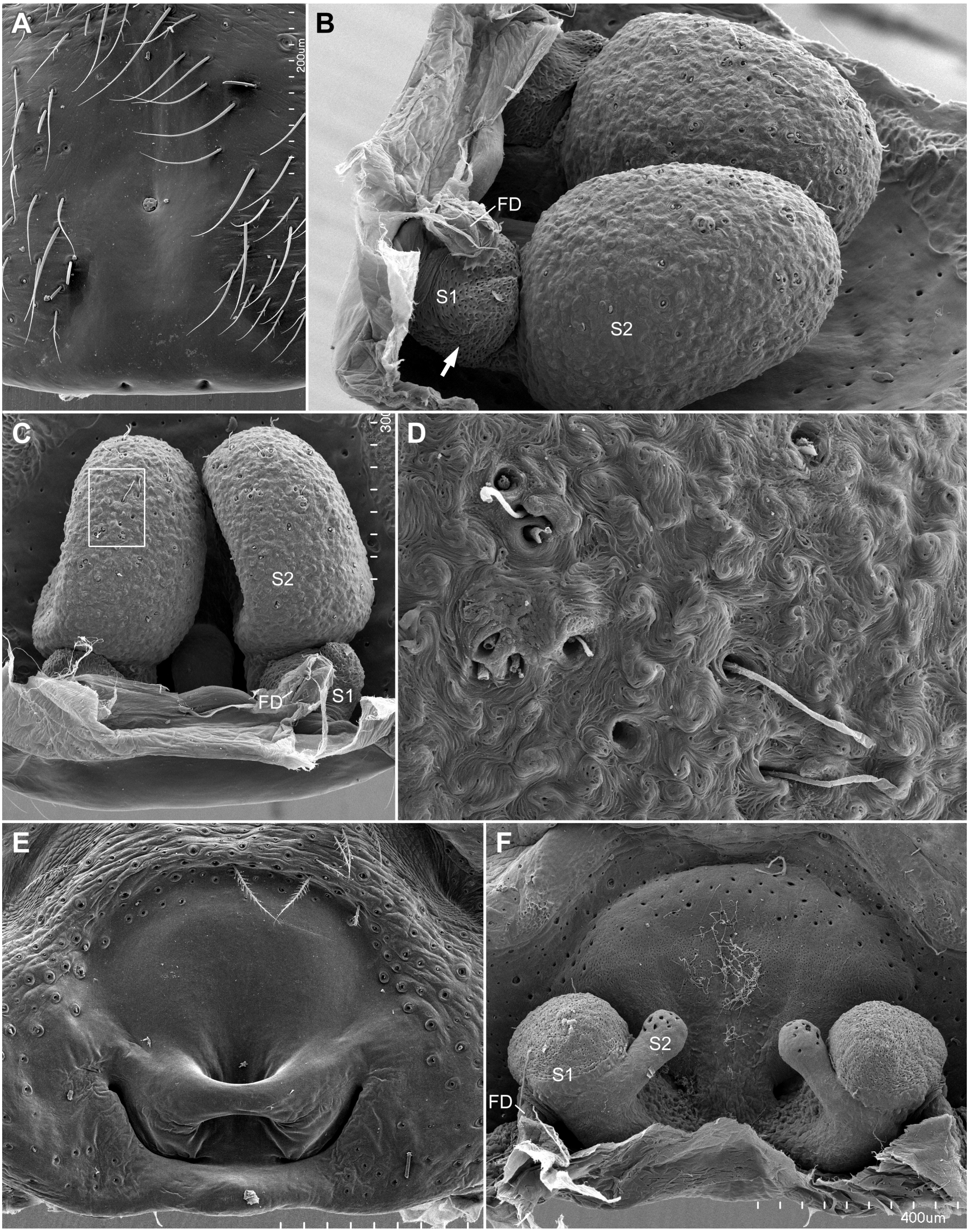

A
200um
B
FD
S1
S2
C
300
S2
FD
S1
D
E
F
S2
S1
FD
400um

Fig. 177. Structures of female genitalia of Corinninae. **A.** *Corinna bulbula*, ventral. **B.** Same, dorsal lateral, arrow to dense patch of pores. **C.** Same, dorsal, marked inset on S2 detailed in D. **D.** Same, detail of gland ducts on S2. **E.** *Creugas gulosus* ventral. **F.** Same, dorsal.

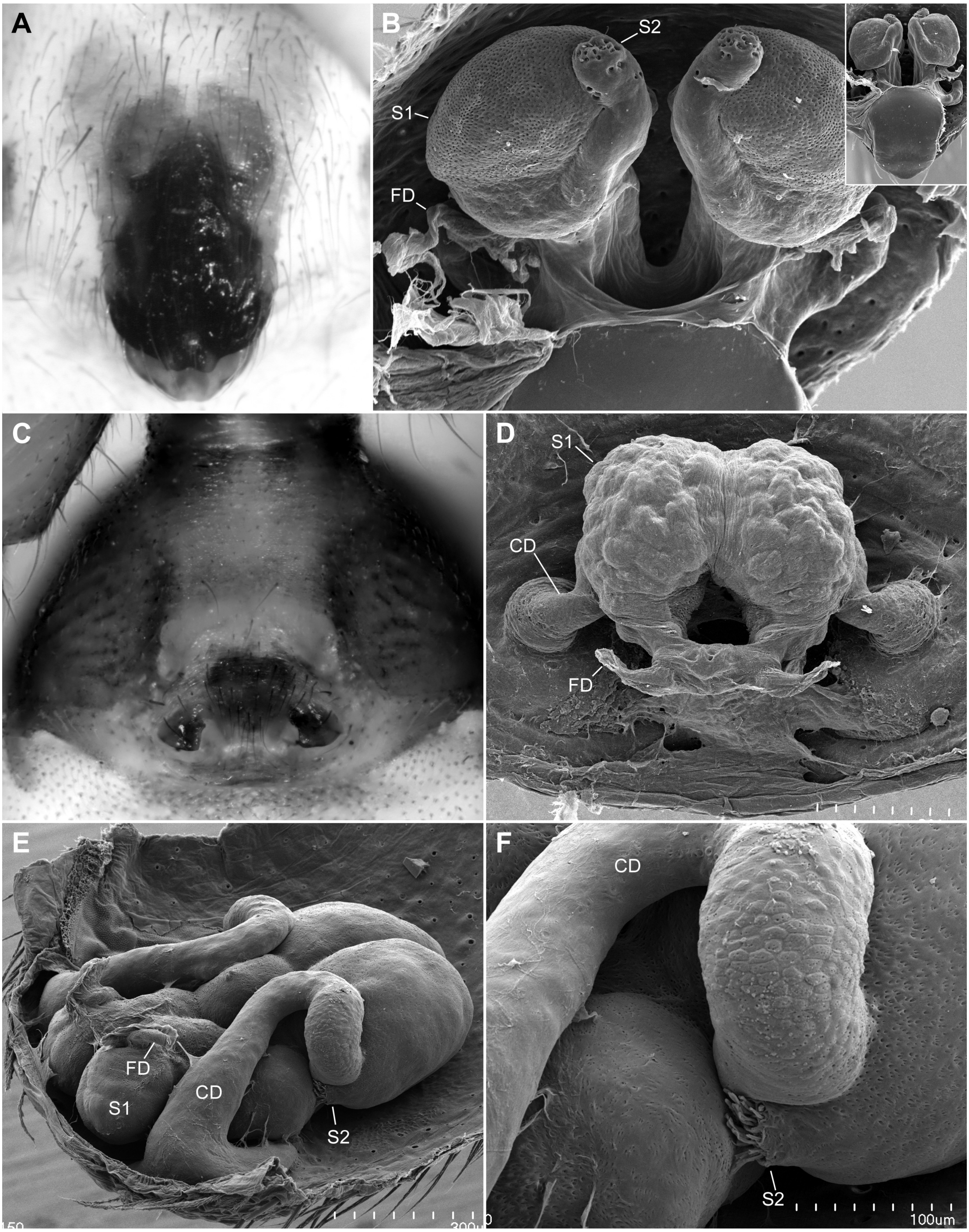


Fig. 178. Structures of female genitalia of Corinnidae. **A.** *Falconina gracilis* (Corinninae) ventral. **B.** Same, detail dorsal anterior, inset showing complete genitalia. **C.** *Castianeira* sp. Iguazu (Castianeirinae) ventral. **D.** *Castianeira trilineata* (Castianeirinae) dorsal, the S2 not exposed in this image. **E.** *Copa flavoplumosa* (Castianeirinae) dorsal lateral. **F.** Same, detail.

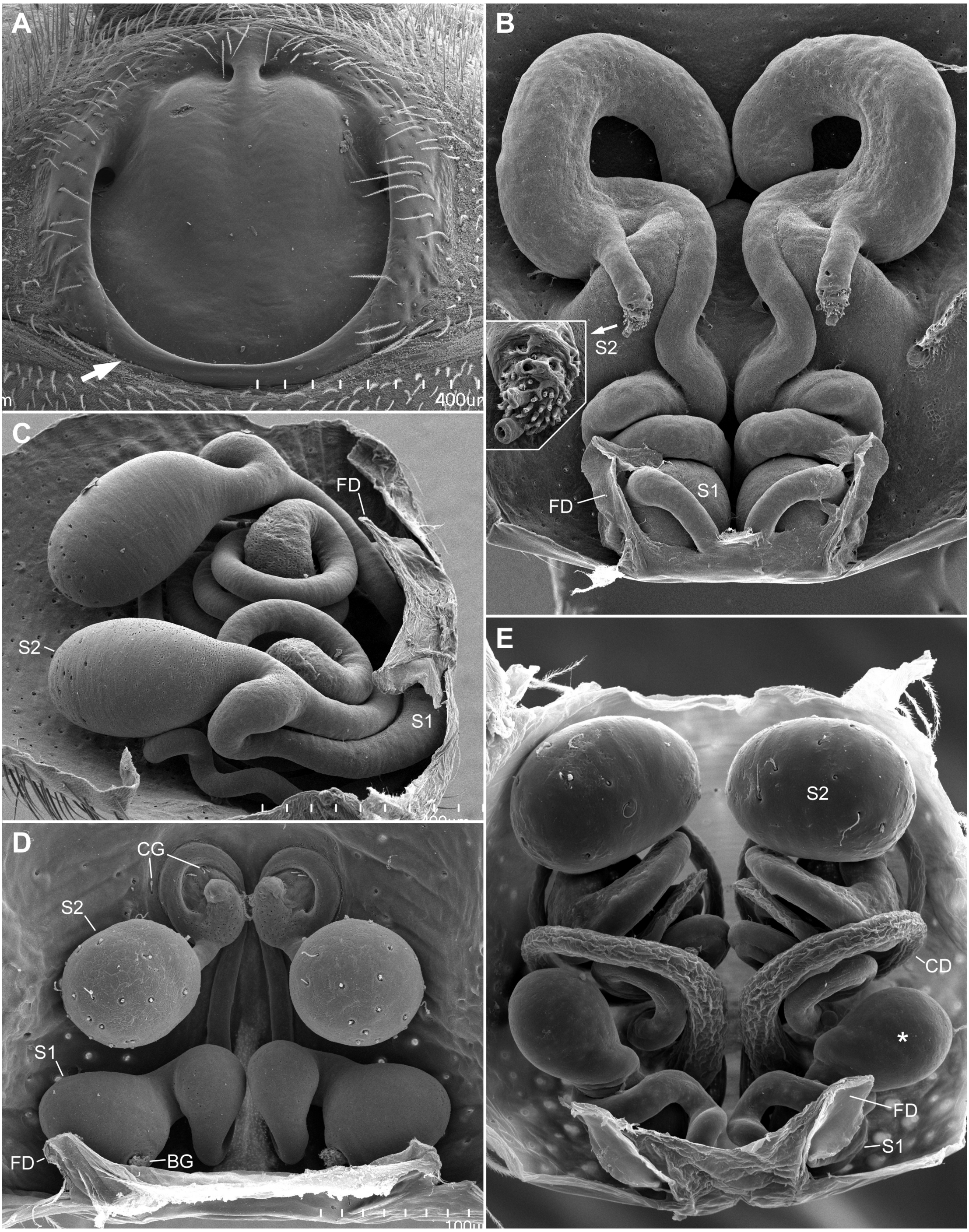

A
B
S2
S1
FD
C
FD
S2
S1
D
CG
S2
S1
FD
BG
E
S2
CD
*
FD
S1

Fig. 179. Structures of female genitalia of Trachelidae. **A.** *Meriola barrosi* ventral, arrow to epigastric furrow. **B.** *Paccius* cf. *scharffi* dorsal. **C.** *Trachelas mexicanus* dorsal lateral. **D.** *Trachelas minor* dorsal. **E.** Trachelidae ARG, dorsal, asterisk on receptacle in CD.

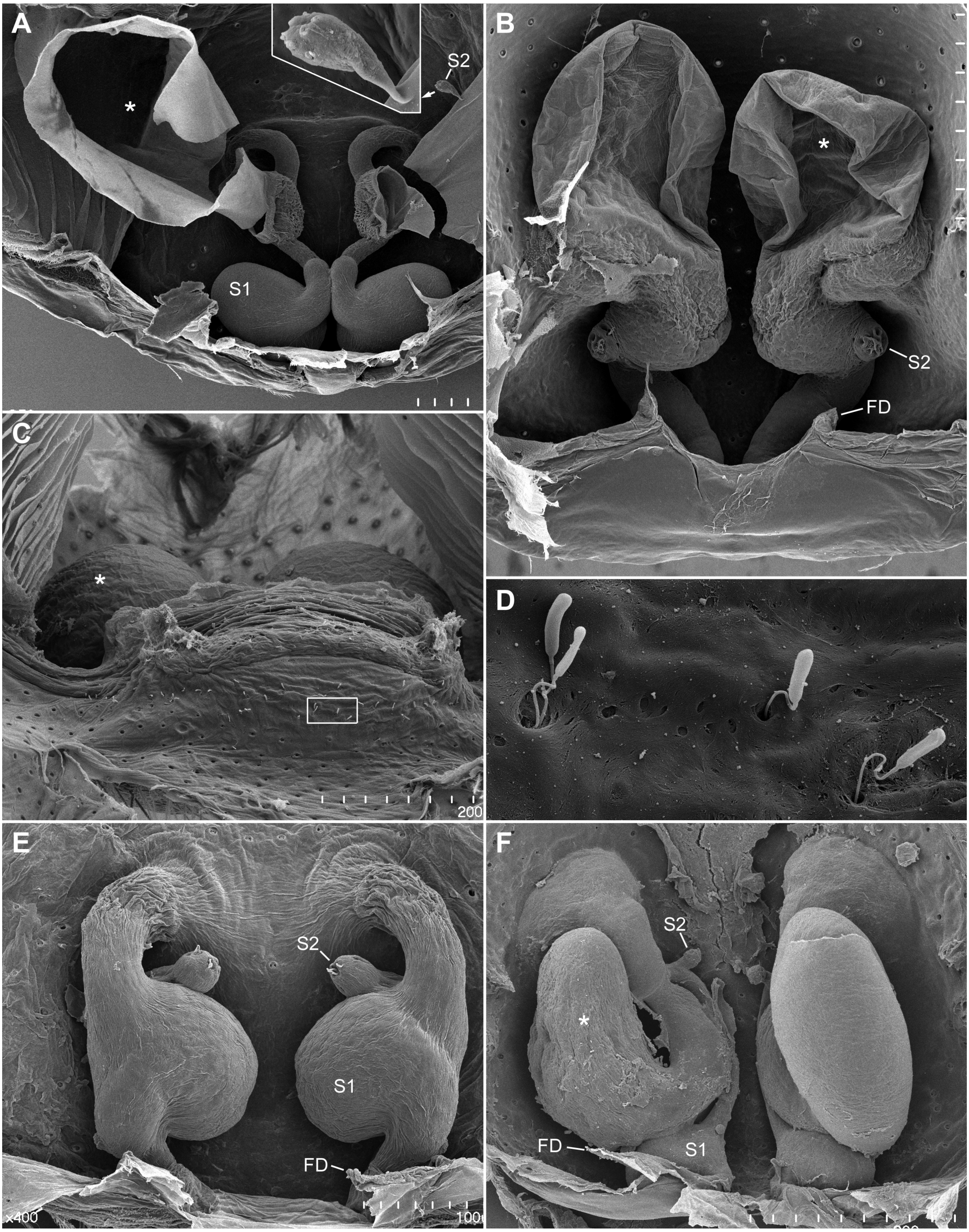


Fig. 180. Structures of female genitalia of Phrurolithidae. **A.** *Orthobula calceata* dorsal. **B.** *Otacilia* sp. dorsal. **C.** *Phrurolithus festivus* dorsal posterior, inset detailed on D. **D.** Same, detail of ducts of cuticular glands. **E.** *Drassinella gertschi* dorsal. **F.** *Phrurotimpus alarius* dorsal. (Asterisks to globose membranous extension of proximal copulatory duct.)

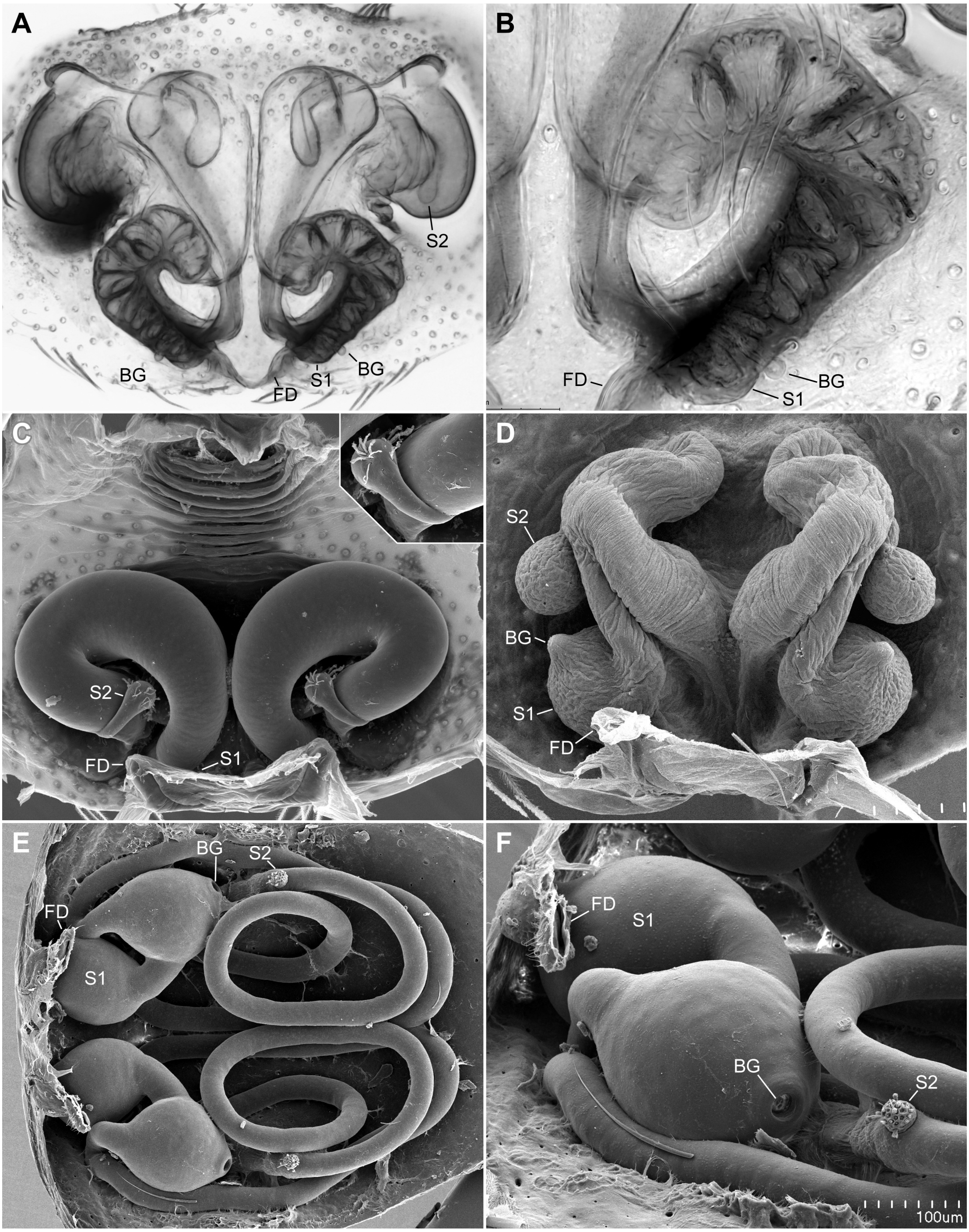

A
S2
BG
FD
S1
BG
B
FD
BG
S1
C
S2
FD
S1
D
S2
BG
S1
FD
E
BG
S2
FD
S1
F
FD
S1
BG
S2
100um

Fig. 181. Structures of female genitalia of members of the CTC Clade and the *Teutamus* group (Liocranidae). **A.** *Xenoplectus* sp. ("Gnaphosidae") dorsal cleared, with visible everted Bennett's gland. **B.** Same, detail of left spermatheca. **C.** Cf. Liocranidae LIB, dorsal, inset to left S2. **D.** *Toxoniella* sp. (Liocranidae) dorsal. **E.** *Jacaena* sp. (Liocranidae) dorsal. **F.** Same, dorsal-lateral.

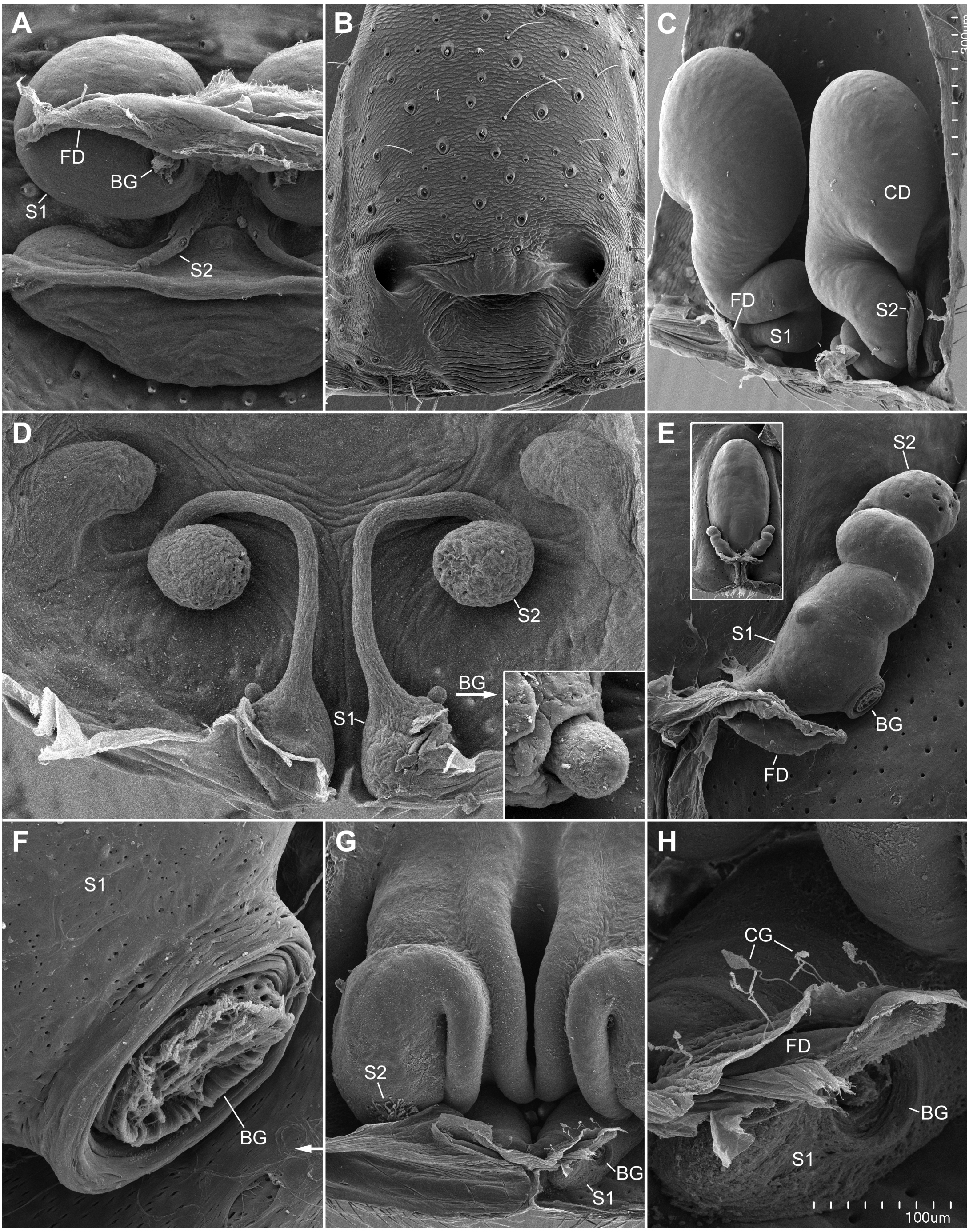

A
FD
BG
S1
S2
B
C
300um
CD
FD
S2
S1
D
S2
BG
S1
E
S2
S1
BG
FD
F
S1
BG
G
S2
BG
S1
H
CG
FD
BG
S1
100um

Fig. 182. Structures of female genitalia of Gnaphosoidea. **A.** *Ammoxenus coccineus* (Ammoxenidae) dorsal anterior. **B.** *Cithaeron delimbatus* (Cithaeronidae) ventral. **C.** Same, dorsal lateral. **D.** *Legendrena perinet* (Gallieniellidae) dorsal. **E.** *Lampona cylindrata* (Lamponidae) dorsal, left spermatheca. **F.** Same, detail of Bennet's gland. **G.** *Centrothele mutica* (Lamponidae) dorsal. **H.** Same, detail of fertilization duct with cuticular gland ducts, and Bennet's gland.

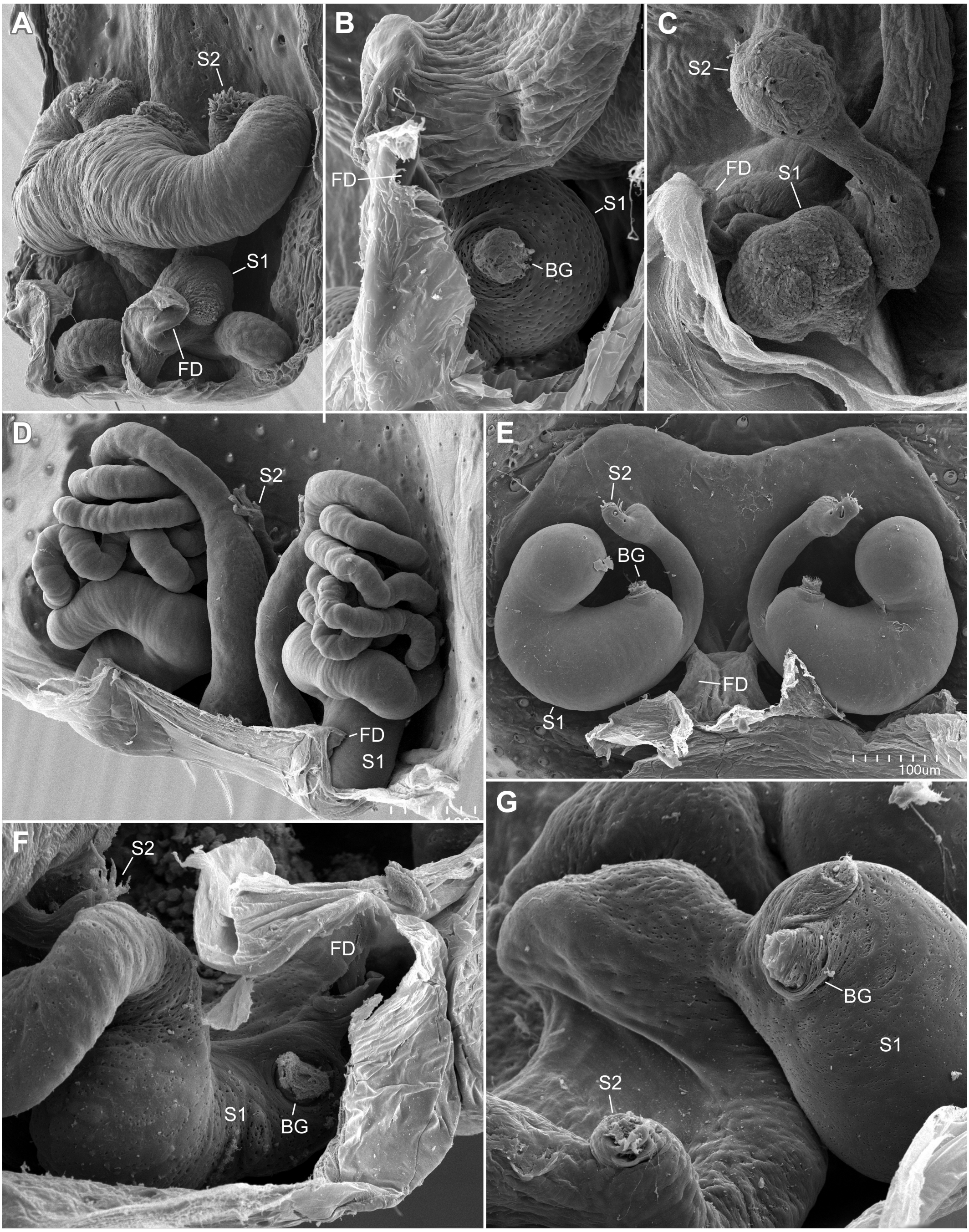

A
S2
S1
FD
B
FD
S1
BG
C
S2
FD
S1
D
S2
FD
S1
E
S2
BG
FD
S1
100um
F
S2
FD
S1
BG
G
BG
S1
S2

Fig. 183. Structures of female genitalia of Gnaphosoidea. **A.** *Desognaphosa yabbra* (Trochanteriidae) dorsal lateral. **B.** *Doliomalus cimicoides* (Trochanteriidae) dorsal lateral, left spermatheca and Bennett's gland. **C.** *Anagraphis pallens* (Prodidomidae) dorsal lateral, right spermatheca. **D.** *Lygromma* sp. (Prodidomidae) dorsal lateral. **E.** *Micaria fulgens* (Gnaphosidae) dorsal. **F.** *Eilica* sp. (Gnaphosidae) dorsal lateral, left spermatheca and Bennett's gland. **G.** *Camillina calel* (Gnaphosidae) dorsal lateral, left spermatheca and Bennett's gland.

FERTILIZATION DUCT: The fertilization duct connects the primary spermatheca to the uterus externus (fig. 169A). The cuticle of the epigastric fold covers the posterior-dorsal section of the epigyne between the posterior margin and the fertilization ducts (fig. 168C), even when the primary spermathecae are placed well in advance of the epigastric fold (fig. 169D).

POSTERIOR RECEPTACLE: Some haplogyne Araneomorphae (e.g., Dysderoidea) have a receptacle posterior to the uterus externus, arising from the posterior wall of the epigastric fold (fig. 167F). The posterior receptacle may be supplied by glands or osmoregulatory structures with cuticular ducts (Izquierdo and Labarque, 2010).

363. Gonopore position relative to epigastric furrow: 0. Internal, the gonopore is not visible externally (figs. 167B, 179A). 1. Anterior, exposed (fig. 170A). See Griswold et al. (2005: char. 135).

364. Epigynum: 0. Absent, the female epigastrium is not elaborated (fig. 167A). 1. Present, the female epigastrium have surface elaborations, often sclerotized, which may occur in spiders with entelegyne or haplogyne genital system (figs. 170A, 179A). See Griswold et al. (2005: char. 131).

365. Epigynum lobes: 0. Median field and lateral lobes delimited by furrows (figs. 171F, 176E) or sutures (figs. 167C, 176A). 1. Undivided plate, suture not visible (fig. 177A). The suture between median field and lateral lobes is usually most conserved at the posterior margin of the epigynum. COMMENTS: *Oecobius*: suture also absent in *Uroctea* (scored 1). *Oxyopes*: at least undefined posteriorly (scored 1). *Dolomedes*: delimited, after Sierwald (1989) (scored 0). *Elaver*: sutures converging on posterior margin (scored 1). *Donuea*: not scanned (scored ?). *Trachelas minor*: suture visible (fig. 167C) (scored 0). *Meriola*: suture visible (scored 0). *Paccius*: only anterior part of suture (scored 1). *Procopius*: similar to *Pseudocorinna* in the posterior displacement of the epigynum (scored 0). *Otacilia, Cithaeron*: no suture but change in texture (fig. 182C) (scored 1). *Drassinella*: from Platnick and Ubick (1989: fig. 7) (scored 0). *Oedignatha*: median field membranous (scored 0). *Anagraphis*, *Centrothele*: lateral lobes very close to each other (scored 0). *Malenella*: suture visible (fig. 176A) (scored 0). *Systaria*: very faint suture (scored 01). *Lauricius*: with a scape (scored 0). *Stephanopoides*: furrows or sutures absent posteriorly (scored 01). *Aphantochilus*: very much advanced (scored 1).

366. Epigynum teeth on lateral lobes: 0. Absent. 1. Present (figs. 171A, 172D, F, 173E). COMMENTS: *Uloborus*: unclear homology of the posterior projections (scored ?). *Metaltella*, *Neoanagraphis*, *Borboropactus*: well advanced (figs. 171A, 172D, 173E) (scored 1). *Neoramia*: small teeth on median field (not on lateral lobes) (scored 0). *Cyrioctea*: something similar to teeth in *C. spinifera* but not in *C. aschaensis* (scored 01). *Senoculus*: the teeth are well advanced, pointing anteriorly; note that the lateral lobes are so projecting that the muscle insertions, normally external, are between the lateral lobe horns (scored 1). *Raecius*: the teeth in some *Raecius* are anterior (scored 01). Sparianthinae VEN: thicker than in other taxa (scored 1). *Eutichurus*, *Mituliodon:* lateral lobes with anterior flat convergent projections (fig. 175A, G) (scored 0). Miturgidae QLD, *Miturga gilva*: similar projections as in *Mituliodon*, but much shallower.

367. Epigynum posterior extension: 0. Not extending much beyond the epigastric furrow (fig. 177E). 1. Evidently projecting posteriorly (figs. 170E, 178B).

368. Mating plug–epigyne interaction: 0. Mating plug small or absent. 1. Mating plug extending laterally over epigastrium (figs. 167E, 171D, E). 2. Two epigynal cavities filled by plugs, with median septum (figs. 169E, 172A). In *Ciniflella* BRA the lateral depressions extend below the median scapus (fig. 171B, C). The epigynum of *Cycloctenus* has a field of cuticular extensions seemingly interacting with the mating plug (fig. 172C). On the internal side, that area corresponds to a high concentration of epigynal glands (fig. 169C) (the same association occurs in *Brachyphaea*). *Toxopsiella* has epigynal glands at the margins of the depressions (fig. 172B). 3. Median cavity filled by mating plug (fig. 176A). In *Macerio* species the plug occupies specific chambers of the copulatory duct and a variable part of the median depression (fig. 175H; Ramírez et al., 1997: figs. 52–54). The presence of the mating plug was recorded but not considered as an active character. Because this study was in large part based on a small series of specimens, the absences are not reliably documented (see review in Uhl et al., 2010). The specific conformations documented in this character are more reliably scored. COMMENTS: *Titanoeca*: small mating plug (scored 0). *Toxopsiella*: not extending but massive (fig. 172A) (scored 0). *Cheiracanthium*: *C. inclusum* with mating plug (scored 0). *Macerio*: mating plugs sometimes occupying a large portion of median depression (Ramírez et al., 1997: fig. 54) (scored 03). Eutichuridae MAD: there is a median cavity, but plug not recorded, few females examined (scored ?). *Pimus*, *Storenomorpha*, *Pseudoctenus*, *Cycloctenus*, *Elaver*, *Castianeira*, *Copa*, *Brachyphaea*, *Paccius*, *Procopius*, *Mandaneta*, *Agroeca*, *Apostenus*, *Xenoplectus*, *Phrurolithus*, *Otacilia*, *Sesieutes*, *Centrothele*, *Malenella*, *Cheiramiona*, *Systaria*, *Lauricius*, *Liocranoides*, *Griswoldia*, *Tibellus*, *Cocalodes*: with mating plugs (scored 0). *Ciniflella* BRA: mating plug filling the holes at the sides of the median field (scored 0).

369. Primary spermathecae fused to each other in midline: 0. Separated (fig. 174E). 1. Fused to each other (figs. 170F, 174C, 178D). COMMENTS: *Filistata*: not individuated, but separate nonetheless (scored 0). *Oecobius*: contiguous, here interpreted as the section 3 of the fertilization duct (B3) in Baum (1972) (scored 0). *Mimetus*: slightly fused (fig. 170F) (scored 1). *Huttonia*: too modified (scored ?). *Megadictyna*: Spermathecae from Harvey (1995) (scored 0). *Calacadia*: contiguous (scored 0). *Storenomorpha*: ducts fused for a while (scored 0). *Clubiona*: only close to each other (scored 0). Cf. *Moreno* ARG: contiguous (scored 0). Cf. Gnaphosoidea TEX: ducts fused, spermathecae separated (scored 0). *Neato*: not dissected, from Platnick (2002: fig. 96), interpreted after the SEM taken from the very similar *Meedo* (scored 0). *Xiruana*: ducts fused, but spermathecae separated (scored 0). *Borboropactus*: connected by a sclerotized fold (scored 0).

370. Bennett's gland insertion: 0. Depressed or superficial (figs. 163B, 168D). 1. Everted (figs. 168E, 181A, B, D, 182D, 183B, E, G). The "dictynoid" pore was first documented by Bennett (1992). Because this structure is not specific of Dictynoidea (see Forster, 1970), here it is referred to as *Bennett's gland*. The pore area is often placed in areas not exposed (e.g., between the spermatheca and epigyne cuticle, hidden by the copulatory duct), and it is hard to detect with transmitted light. The presence or absence of Bennett's glands was preliminarily recorded, but those observations are not reliable for documenting absences. This character is more reliably scored. Haplogynes and entelegynes where the glands are apparently absent were scored as inapplicable. COMMENTS: *Macrobunus*: primary spermatheca not well exposed (scored ?). *Cyrioctea*: very large porous plate (scored 1). *Dictyna*: presumed absent by Bennett (1992), not examined in detail (scored ?). *Senoculus*: not found with compound microscope (scored ?). *Clubiona*: large porous plate (scored 1). *Elaver*: Area not exposed. Another species from Costa Rica with pore plate not well delimited (fig. 173D) (scored ?). *Donuea*: primary spermatheca not well exposed, not seen with the compound microscope (scored 0). *Corinna*, *Castianeira*, *Brachyphaea*, *Cheiramiona*: porous area not clearly homologous (scored 0). *Hortipes*: may be everted in some species, see figures in Bosselaers and Jocqué (2000) (scored ?). *Gnaphosa*: *G. taurica*, apparently everted, but not clean preparation (scored 01). *Eilica*, *Apodrassodes*, *Lampona*: slightly everted (figs. 182E, F, 183F) (scored 01). *Centrothele*: only the center protruding (scored 0). *Neozimiris*: pore area not well delimited (scored ?). *Meedo*: primary spermatheca not exposed, not seen with the compound microscope (scored ?). *Cithaeron*: one side with ambiguous structure on compound microscope (scored 0). *Desognaphosa*: bulging porous area without clear limits (fig. 183A) (scored 0). *Systaria*: a porous plate not well delimited (scored 01).

371. Primary pores of secondary spermatheca: 0. Present (figs. 178A, 179B). The pores and ducts may be present, without a delimited receptacle (figs. 173C, 176B). 1. Absent (fig. 171G). The ducts are well preserved after digestion; there may be patches of pores without sclerotized ducts, not considered homologous here (fig. 174D). The primary pores (after Bennett, 1992) are located at the end of a blind tube, the secondary spermatheca (= head of spermatheca). COMMENTS: *Oecobius*: secondary spermatheca here interpreted as the receptaculum in Baum (1972) (scored 0). *Uloborus*: large pores on main reservoir, but ducts not checked with SEM (scored 01). *Araneus*: pores without ducts (scored 1). *Mimetus*: only the ducts observed, dirty preparation (scored 0). *Huttonia*: the primary pores are well defined, over the median receptacle, at the base of the apodeme, but not on the multiple lateral heads (scored 0). *Eriauchenius*: on the large receptacles (scored 0). *Stiphidion*: examined with compound microscope (scored 1). *Senoculus*: pores not seen with compound microscope, but large secondary spermatheca reported for *Senoculus canaliculatus* by Griswold (1993). *Pseudocorinna*: not seen but very complex, possible ducts on anterior side of spermatheca (scored ?). *Xenoplectus*, *Hortipes*, *Prodidomus*: examined with compound microscope (scored 0). Trachelidae ARG: a few pores on the anterior round receptacles (scored 0). *Sesieutes*: On ventral side of copulatory duct, close to the copulatory opening (scored 0). *Trachycosmus*: so complex, preparation shrunken (scored 0). *Pseudolampona*: not seen in compound microscope (scored ?). *Malenella*: the ducts and pores are present, but without a delimited receptacle (fig. 176B) (scored 0). Cf. Eutichuridae QLD: vulva similar as in *Malenella* (scored 0). *Epidius*: not distinguishable with the compound microscope (scored ?). *Stephanopoides*: not seen in SEM (scored ?). *Tmarus*: on copulatory duct, but not well defined patch (scored 0). *Strophius*: perhaps on distal copulatory duct (scored ?). *Thomisus*: perhaps on dorsal side of vulva, not examined in SEM, ambiguous on compound microscope (scored ?). *Portia*: only a porous area at the junction of copulatory duct with primary spermatheca (fig. 174D) (scored 1).

372. Lumen of secondary spermatheca: 0. Secondary spermatheca a blind sac with defined lumen. Most usually the secondary spermatheca (= head of spermatheca) has a well-defined lumen and connects to the copulatory duct via a duct (figs. 177C, D, 180A, 181C, 182B). 1. Secondary spermatheca a pore field without its own lumen (figs. 173C, 176C, D, 178F, 182G). COMMENTS: *Filistata*: not clear which one of the two receptacles may be homologous with the secondary spermatheca (scored ?). *Corinna*: the main reservoir (scored 1). *Orthobula*: arising from the huge globose receptacle! (scored 0). *Otacilia*, *Jacaena*, *Meedo*, *Philodromus*, *Anyphops*, *Heteropoda*: very short duct, but secondary spermatheca well delimited (scored 0). *Malenella,* cf. Eutichuridae QLD: the gland ducts connect to a small patch of pores in a bulbous camera which I interpreted as a widened copulatory duct (scored 1). *Plexippus*: small secondary spermatheca lateral to copulatory duct (fig. 174F) (scored 0).

373. Secondary spermatheca size, relative to primary spermatheca: 0. Smaller than primary spermatheca (figs. 173F, 174E, 181F, 183D). 1. About as large as primary spermatheca (figs. 179D, 182D, 183C). 2. Larger than primary spermatheca (figs. 175B, E, 177C, 179C, E). States are ordered. This character was considered applicable when the secondary spermatheca has a lumen defined from the copulatory duct or primary spermatheca. In some groups (e.g., Trachelidae, some Corinninae) the secondary spermatheca seems to have taken over the function of main sperm receptacle, instead of the primary spermatheca. COMMENTS: *Clubiona*: larger in some other *Clubiona* species; *Clubiona corticalis* very similar to *Orthobula* (Wiehle, 1965) (scored 0). *Lampona*: although primary spermatheca quite small as well (scored 0). Sparianthinae VEN: intermediate, secondary spermatheca smaller but still large (scored 01).

374. Receptacle in copulatory duct, in addition to primary and secondary spermathecae: 0. None, copulatory duct lumen not expanded in a receptacle additional to primary and secondary spermathecae (fig. 180E). 1. Copulatory duct widened, forming a defined chamber between the copulatory opening and primary spermatheca (figs. 173B, 178E, 180A, B, F, 181E, F). This character was considered applicable for entelegyne configuration, where the copulatory duct is clearly delimited. COMMENTS: *Metaltella*: two additional receptacles (scored 1). *Calacadia*: the copulatory duct forms a chamber just before the primary spermatheca (fig. 179E) (scored 1). *Aglaoctenus*: similar as the "bulbal chamber" in *Sossipus* (Sierwald, 2000; Santos and Brescovit, 2001) (scored 1). *Clubiona*: blind lateral lobes close to copulatory opening (lateral pouches in Huber, 1995b; see also Whiele, 1965) (scored 1). *Castianeira*: large multichambered receptacle, all in one piece (scored ?). *Copa*: the copulatory duct is well expanded at the area where the secondary spermatheca is attached (fig. 178E) (scored 1). *Trachelas minor*: copulatory duct slightly widened before SP1 (scored 01). *Meriola*: anterior blind sac not well defined, but conspicuous in other species (Platnick and Ewing, 1995) (scored 01). *Trachelopachys*: stalked receptacle (scored 1). *Procopius*: all too short (scored ?). Trachelidae ARG: just before primary spermatheca (scored 1). *Jacaena*: primary spermatheca divided in two, one piece has the "dictynoid" pore, the other the fertilization duct (fig. 181E, F) (scored 1). *Vectius*: SP1 tentatively identified after a wide pore plate, interpreted as Bennett's gland pores (scored 0). *Macerio*: only the chamber for the mating plug (scored 0). *Aphantochilus*: just where the secondary spermatheca is attached, connected to primary spermatheca through constriction (scored 1).

375. Globose membranous extension of proximal copulatory duct: 0. Absent. 1. Present. The proximal copulatory duct, before the connection of the secondary spermatheca, has a globose, well-delimited diverticulum with flexible walls (fig. 180A, B, F). This character was considered applicable for entelegyne configuration, where the copulatory duct is clearly delimited. COMMENTS: *Oecobius*: the secondary spermatheca itself is globose, and not proximal (scored 0). *Clubiona*: not so globose (fig. 173B) (scored 01). *Donuea*: looks like a membranous sack, entangled with the copulatory duct, not globose (scored 0). *Orthobula*: secondary spermatheca arises from globose extension! (fig. 180A) (scored 1). *Eilica*: just widened proximal ducts (scored 0). *Cithaeron*: wide expansion of copulatory duct, sclerotized (scored 0). *Thomisus*: the entire primary spermatheca is membranous (scored 0). *Hispo*: the globose receptacle is on distal copulatory duct, after connection of secondary spermatheca (scored 0).

376. Cuticular glands on epigyne: 0. Absent. 1. Present. The cuticular glands found in the epigyne have a chitinous duct running through a pore in the cuticle. The duct remains after digestion with enzymes or KOH (figs. 169C, E, 174G). Besides having a duct, the gland pores are much smaller than those that are connected to setae. The gland ducts may have an expansion (figs. 175C, 180D) and vary in length (fig. 175F). It is common to find the glands extending over the proximal copulatory ducts (fig. 171G, H). The glands were previously figured by Griswold in *Phanotea* (1994: figs. 6, 8). In some taxa there seems to be an association between the placement of the glands and the attachment of the mating plug (see char. 368 above). The glands seem not specific to the epigyne, as several terminals have many of them on the posterior wall of the epigynal fold (figs. 169A, 180C, D, 182G, H) and on the abdomen in general (Alvarez Padilla, personal commun.). COMMENTS: *Ariadna*: not found in *A. maxima*, *A. mollis* (scored 0). *Calacadia*: especially around the copulatory opening (scored 1). *Cybaeodamus*: on copulatory duct (scored 1). *Paradiestus*: many gland ducts on epigastric fold, especially on posterior wall (fig. 169A). *Brachyphaea*: concentrated in the area for the mating plug (scored 1). *Procopius*: they might occur where the plugs do, not accessible in preparation (scored ?). *Phrurolithus*: cuticular glands posterior to the epigastric fold (fig. 180C, D), epigynal area not scanned (scored ?). *Teutamus*: only one seen (scored 01). *Gnaphosa*: present in *G. sericata*, bad preparation for *G. taurica* (scored 1). *Apodrassodes*: not clean preparation (scored ?). *Neozimiris*: bad preparation (scored ?). *Centrothele*: glands on fertilization duct! (fig. 182G, H) (scored 0). *Platyoides*: on anterior depression (scored 1). *Syspira*: perhaps some on proximal copulatory duct (scored ?). *Raecius*: visible in Griswold (2000: fig. 42) (scored 1). *Zorocrates*: a few close to the copulatory openings (scored 1). *Ciniflella* ARG: on proximal copulatory ducts (scored 1). *Heteropoda*: a few on the fertilization duct (scored 0). *Anyphops*: at least on fertilization ducts (scored 1). Sparianthinae VEN: on the copulatory openings (scored 1).

377. Copulatory duct between primary and secondary spermathecae: 0. None, confluent. The secondary spermatheca and the copulatory duct connect to the primary spermatheca at the same point, or both directly on the primary spermatheca (figs. 172E, 173B, 177F, 182A). 1. Distinct. The secondary spermatheca connects to the copulatory duct, which afterward runs for a length before joining the primary spermatheca (figs. 172G, 174A, 179B). COMMENTS: *Syspira*: one of the females MJR-496 to 498 dissected for tracheae has an embolus stuck inside, reaching up to (or close) to the spermatheca (scored 1). *Tmarus*: the sector of the copulatory duct where secondary spermatheca is located is wide, containing sperm, not clear limit with primary spermatheca (scored 01).

378. Fertilization ducts: 0. Absent, haplogyne (fig. 168B). 1. Present, entelegyne (figs. 168D, 176F). COMMENTS: *Oecobius*: not illustrated in Baum (1972), but observed with compound microscope (scored 1). *Stephanopoides*: also a posterior sclerotized rod uniting the primary spermatheca with the epigastric fold (scored 1).

379. Fertilization duct position: 0. Posterior, close to the epigastric furrow (figs. 173C, 174E, 176F, 182D). 1. Well advanced from the epigastric furrow (figs. 169D, 173A, 174B, F). The external cuticle covers a good portion of the vulva in ventral view, from the epigastric furrow to the fertilization duct. This cuticle has to be removed to expose the structures for SEM. COMMENTS: *Pimus*: fertilization duct long, running fused to copulatory duct up to epigastric fold (scored 0). *Lessertina*: midway (scored 01). *Zorocrates*: advanced ("median" according to Griswold, 1993) (scored 0). *Aphantochilus*: the whole epigynum is well advanced, but the ducts are posterior to the vulval elements (scored 01). *Cocalodes*: Wanless (1982) mentions the peripheral objects in epigynum (scored 1).

380. Receptaculum on female posterior atrial wall: 0. Absent, posterior wall of atrial cavity without a well-defined receptacle. The wall can be smooth (fig. 170D) or have an invagination for muscle attachments (figs. 99F, 169A, 170B). 1. Present, the posterior wall leads to a well-defined posterior receptacle (figs. 167F, 170C). Only the segestriid *Ariadna* in this dataset has such a receptacle. COMMENTS: *Thaida*: interpreted as in Griswold et al. (2005) (scored 0). *Huttonia*: there is a posterior flat flap, for muscle attachment (scored 0).

DEVELOPMENT AND BEHAVIOR

381. Adult female molt: 0. Present. Filistatids are the only araneomorphs where females are known to keep molting after maturity (Bonnet, 1939, for *Filistata insidiatrix*; personal obs. for *Kukulcania hibernalis*), as do mygalomorphs and mesothelids. 1. Absent. Females stop molting after reaching maturity. COMMENTS: *Hypochilus*: after Kefyn Catley (personal commun.) (scored 1). *Thaida*: molts are very common in the field, never found one with genitalia (scored 1). *Eriauchenius*: immatures have a suture in the cheliceral diastema, to allow molting; the suture is missing in adult females (Wood et al., 2012: figs. 5a, f) (scored 1). *Ariadna*, *Uloborus*, *Araneus*, *Aglaoctenus*, *Oxyopes*, *Clubiona*, *Gnaphosa*, *Cheiracanthium*, *Anyphaena*, *Philodromus*, *Xysticus*, *Thomisus*, *Portia*: these terminals were so intensely studied that it is presumed that adult molts would have been noticed while rearing them (scored 1).

382. Prey-catching web: 0. Present. 1. Absent. COMMENTS: *Macrobunus*: found in loose silken cells under logs (scored 0). *Cyrioctea*: tubes in sand (scored 01). *Cybaeodamus*: "They live buried on sand, making rather superficial cells, at the base of psammophilic grass. They feed on ants" (Fernando Costa, in litt.) (scored 0). *Dolomedes*: Homann (1971) described the web made by immature *Pisaura* to catch prey; other pisaurids build extensive webs (scored 0). *Teutamus*: many specimens collected wandering on forest litter (scored 1). *Gnaphosa*: just retreats, Vladimir Ovtsharenko, personal commun.; Dacke et al. (1999) (scored 0). *Lampona*: from Forster and Blest (1979) (scored 0). *Ammoxenus*: behavior after compilation by Dippenaar-Schoeman and Jocqué (1997) (scored 0). *Cithaeron*: biology from Russell-Smith in Platnick (1991) (scored 0). *Griswoldia*: from Griswold (1991) (scored 1). *Raecius*: burrows lined with silk (Griswold et al., 2005: fig. 207G) (scored 01). *Portia*: see references in Wanless (1984) (scored 1).

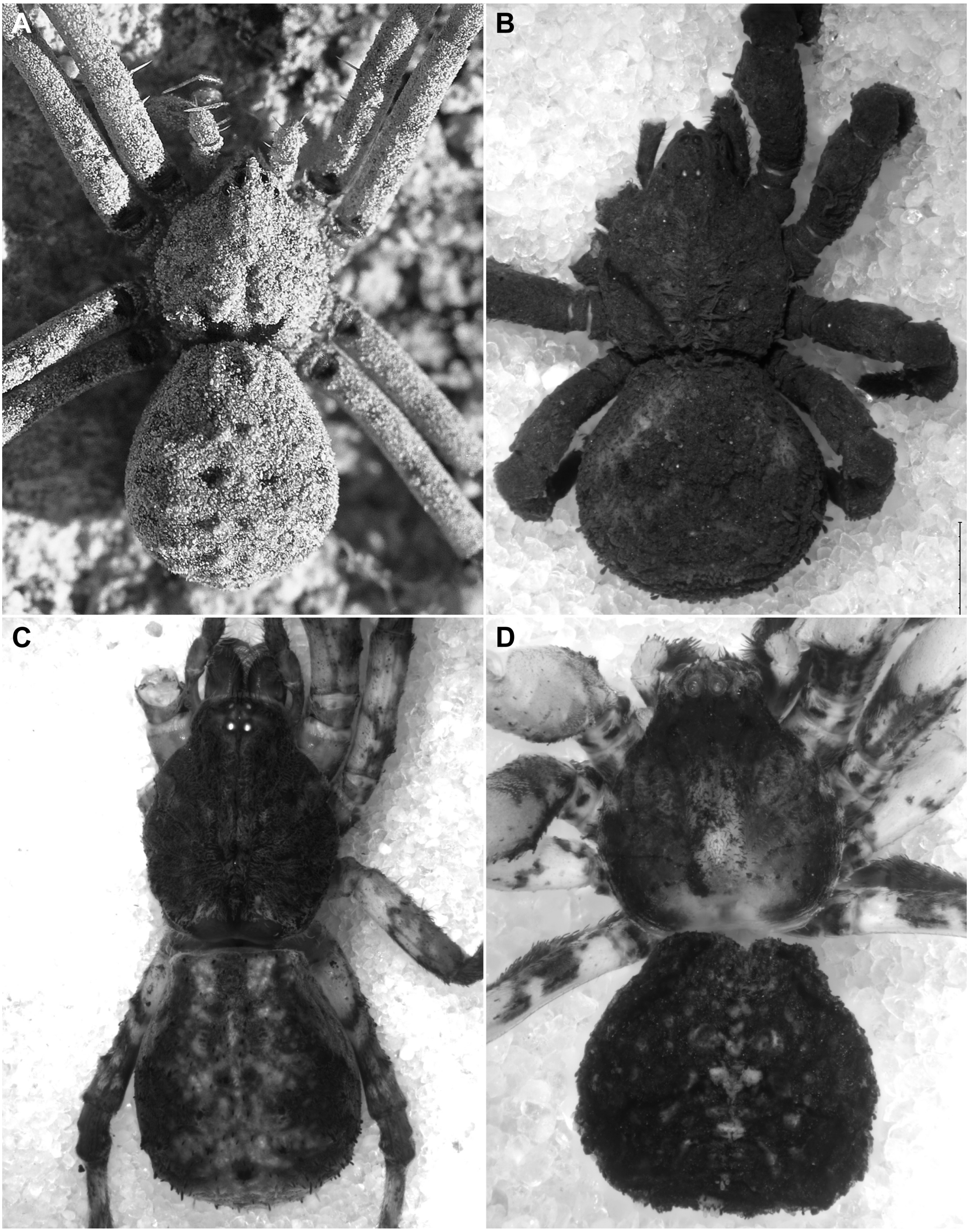


Fig. 184. Habitus of cryptic spiders covered by detritus. **A.** *Homalonychus theologus* (Homalonychidae) penultimate male (photo, by Marshall Hedin). **B.** *Cryptothele* sp. Myanmar (Zodariidae) male. **C.** *Borboropactus bituberculatus* (Thomisidae) female. **D.** *Stephanopis ditissima* (Thomisidae) female.

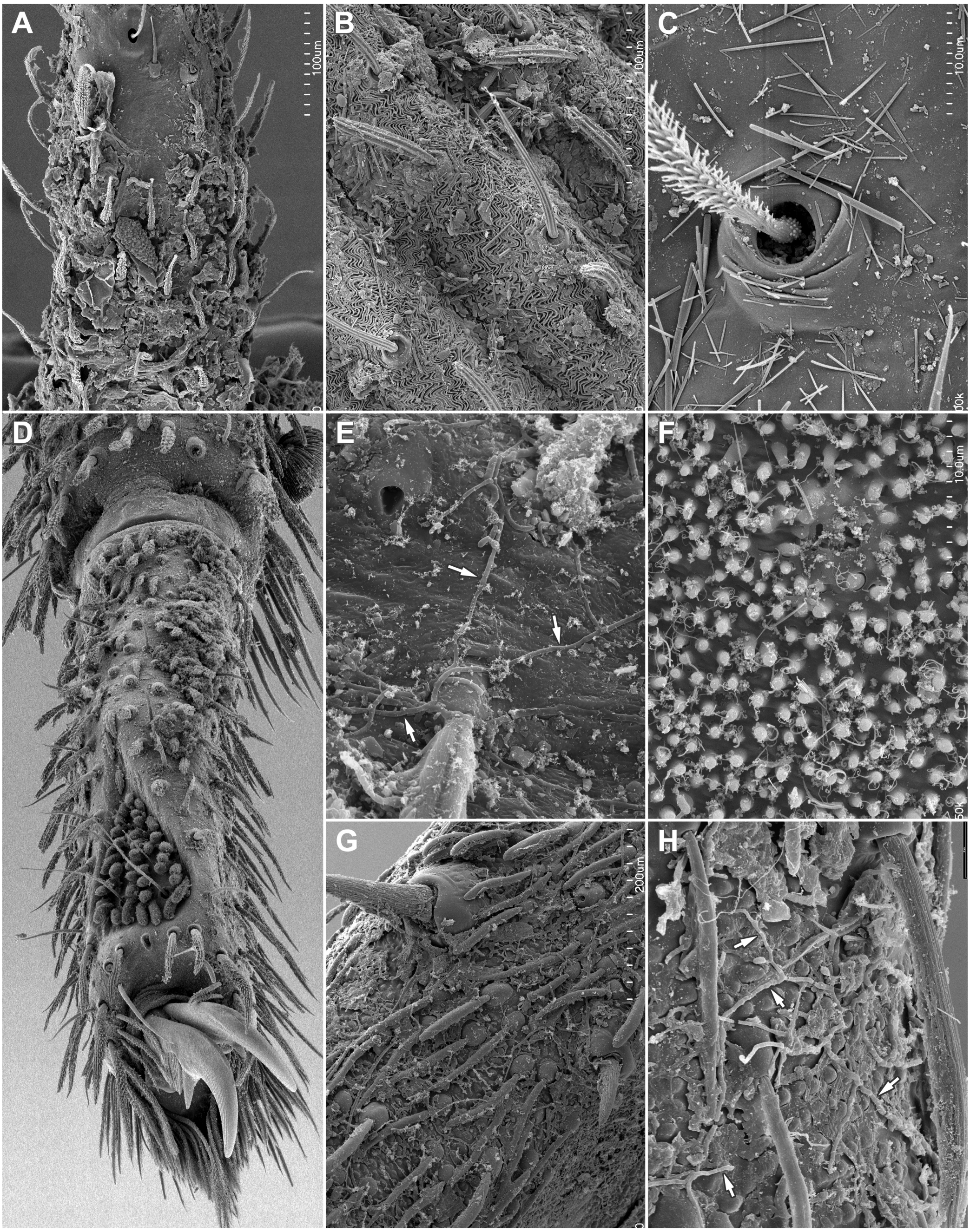


Fig. 185. Cuticle of cryptic spiders covered by detritus and fungi. **A.** *Cryptothele alluaudi* (Zodariidae) immature, right metatarsus I dorsal. **B.** *Cebrenninus rugosus* (Thomisidae) female, abdominal cuticle lateral. **C.** Same, trichobothria from tarsus I. **D.** *Borboropactus bituberculatus* (Thomisidae) female, left tarsus IV dorsal apical. **E.** Same, detail of metatarsus IV showing hyphae (arrows). **F.** *Geraesta hirta* (Thomisidae) female, detail of metatarsus IV dorsal. **G.** *Stephanopis ditissima* (Thomisidae) female, detail of tibia I ventral. **H.** Same, detail of tibia IV retrolateral showing hyphae (arrows).

383. Cribellate silk axial lines: 0. Present. 1. Absent. See Griswold et al. (2005: char. 136).

384. Cribellate silk reserve warp: 0. Present. 1. Absent. See Griswold et al. (2005: char. 137).

385. Cribellar fibrils nodules: 0. Absent. 1. Present. See Griswold et al. (2005: char. 138).

386. Cribellate silk outline: 0. Uniform. 1. Puffed. See Griswold et al. (2005: char. 139).

387. Combing leg support behavior: 0. Immobile, leg III. 1. Mobile, braced leg IV. See Eberhard (1988), Griswold et al. (2005: char. 141) and Lopardo and Ramírez (2007). Representatives with an oval calamistrum (see char. 110) seem to use the same stereotyped movements as their relatives, with mobile, braced legs IV (Griswold et al., 2005: fig. 208D). COMMENTS: *Acanthoctenus*: from Antonio Brescovit (personal commun.) (scored 1).

388. Wrap-bite attack: 0. Absent. 1. Present, bite before wrap. See Griswold et al. (1998: char. 92). COMMENTS: *Galianoella*: from Goloboff (2000) (scored 0).

389. Crypsis through detritus adhesion: 0. Absent. 1. Present (figs. 184, 185). COMMENTS: *Homalonychus*: adhesion through intermolecular forces (Duncan et al., 2007) (scored 1). *Ammoxenus*: some on legs (scored 01). *Geraesta*: most of leg cuticle papillate, with some kind of glue, sticking butterfly scales and some detritus (fig. 185F) (scored 1). *Borboropactus, Stephanopis ditissima*: both detritus and fungi (figs. 95C, 185D) (scored 1).

390. Crypsis with fungi: 0. Absent. 1. Present (figs. 95C, 185E, H). The organisms growing on the cuticle were tentatively identified as fungal hyphae. COMMENTS: *Boliscus*: just a few seen on palp and leg IV (scored 01).

391. Orb web architecture: 0. Absent. 1. Present. See Griswold et al. (2005: char. 142).

392. Ant shielding behavior: 0. Absent. 1. Present. Some thomisids with elongate labium and endites carry the dead bodies of ants as an aggressive mimic strategy (fig. 217). The behavior was described by Oliveira and Sazima (1984, 1985) for *Strophius* and *Aphantochilus*, and for *Bucranium* sp. (now synonymized with *Aphantochilus*) by Bristowe (1941) (see also Cushing, 1997). *Aphantochilus* prey on ants of the genus *Cephalotes* (fig. 217A, B), and *Strophius* on *Camponotus* (fig. 217C, D). The dead ant is presented to the approaching live ants, thus shielding the spider against chemical identification and perhaps helping attract fresh prey.

TABLE 6

Character statistics

Summary statistics for character indices for the preferred tree (fig. 188); s = steps, h = homoplasy, CI = consistency index, RI = retention index, dist = distortion. Global indices are CI = 0.15, RI = 0.51, s = 3006.

	Median	Mean	SD
s	5	9.40	11.55
h	4	8.13	11.23
CI	0.25	0.35	0.31
RI	0.50	0.49	0.32
dist	0.31	0.37	0.38

PHYLOGENETIC ANALYSIS

DATASET AND CHARACTER STATISTICS: The phylogenetic dataset of the final analysis has 393 species scored for 166 characters (table S1, see supplementary material: http://dx.doi.org/10.5531/sd.sp.4). Of the 65,238 cells, 9168 (14%) are inapplicables, 3785 (6%) missing, and 577 (1%) polymorphic. The final analysis includes representatives of 47 families of Araneomorphae (fig. 187), including most of the families whose members have tenent setae, either as claw tufts or as scopulae. The homoplasy levels are moderately high (table 6; table S2 in supplementary material), although the ample difference between median and mean indicates that much of the homoplasy is concentrated in few characters.

SENSITIVITY TO WEIGHTING REGIMES: As expected, the trees from concavities of implied weighting in the middle of the range of weighting strengths (*k* = 9–15) have the greatest number of clades in common with the rest of the weighting regimes (table 7). When groups of marginal Bremer support are filtered out, trees from *k* = 9 share the most groups with all other weighting regimes (cumulative frequency = 1331), without missing most of the optimal groups (cumulative frequency 1439 vs. 1447). For simplicity, the single tree obtained under this concavity is used as the preferred working hypothesis (fig. 188), including a graphical representation of the sensitivity to weighting regimes on each branch (see fig. 186). The

TABLE 7

Shared groups in weighting regimes

For each weighting function, cumulative number of groups shared with the strict consensus trees from all other weighting functions. Results are given for the consensus of optimal trees only (middle) and for the consensus of groups with Bremer support greater than 0.01 units of fit (right). EW = Equal weights. Analyses producing the greatest number of clades in common with the rest of the weighting regimes are in boldface.

Concavity (*k*)	Cumulative frequency	Cumulative Frequency (BS > 0.01)
EW	886	866
3	1229	1056
6	1310	1227
9	1439	**1331**
12	1446	1311
15	**1447**	1288
18	1402	1287
21	1417	1312
24	1429	1323
27	1382	1250

TABLE 8

Homoplasy of setae

Mean consistency index (CI) and retention index (RI) for informative characters, calculated for all the characters, characters from setae in general, and from tenent setae in particular.

Global		Setae		Tenent setae	
N = 393		*N* = 65		*N* = 15	
CI	RI	CI	RI	CI	RI
0.35	0.49	0.26	0.38	0.43	0.78

consensus tree of the analysis under equal weights has important topological differences, especially on the less-supported groups (fig. 189).

SUPPORT OF GROUPS: Bremer support values range from very high values for the most autapomorphic groups (such as Prodidominae, Eresidae, *Mimetus* + *Araneus*) to almost negligible values. Unfortunately, many of the most interesting group hypotheses, such as the root of Dionycha and larger clades within it, are weakly supported. Similarly, only few groups produced resampling frequencies above 50%. High sensitivity to weighting regimes and to changes in additivity of characters is restricted to clades with low Bremer support values (fig. 190). The discussion of groups in the following sections will not pay much attention to clades with low support and very sensitive to weighting regimes, except when they are of specific taxonomic interest.

SENSITIVITY TO ORDERING OF STATES: The alternative codings for ordered characters were examined (table 3). As expected, the groups with weak support are the more affected by alternative cost regimes (fig. 190), and experiment 8, the one with the most ordered characters treated as unordered, is the one that produced the most different results. Several alternative resolutions of taxonomic significance have been included in the comparisons on the following sections (see Thomisidae, Eutichuridae, Miturgidae, Sparassidae, Trochanteriidae, and Ammoxenidae).

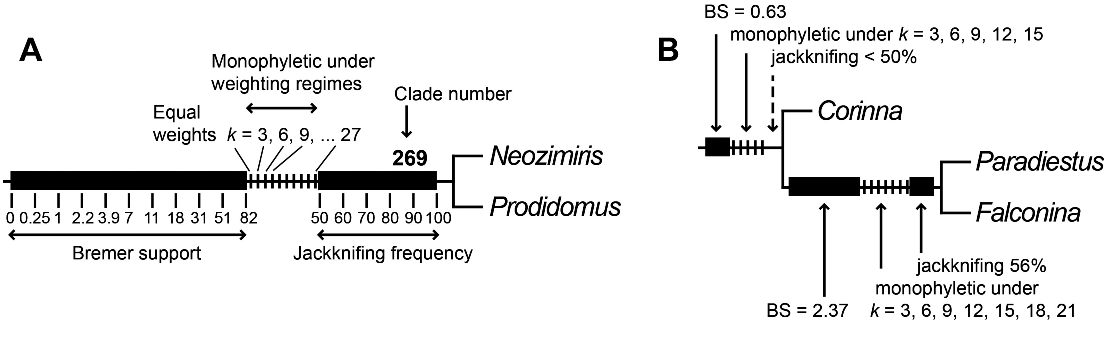

A
Monophyletic under weighting regimes
Clade number
Equal weights
k = 3, 6, 9, ... 27
269
Neozimiris
Prodidomus
0 0.25 1 2.2 3.9 7 11 18 31 51 82
50 60 70 80 90 100
Bremer support
Jackknifing frequency
B
BS = 0.63
monophyletic under k = 3, 6, 9, 12, 15
jackknifing < 50%
Corinna
Paradiestus
Falconina
jackknifing 56%
monophyletic under
k = 3, 6, 9, 12, 15, 18, 21
BS = 2.37

Fig. 186. Branch lengths in cladograms are proportional to a compound measure of support and robustness to changes in weighting regimes. **A.** Scales and conventions. **B.** Examples of values for two clades.

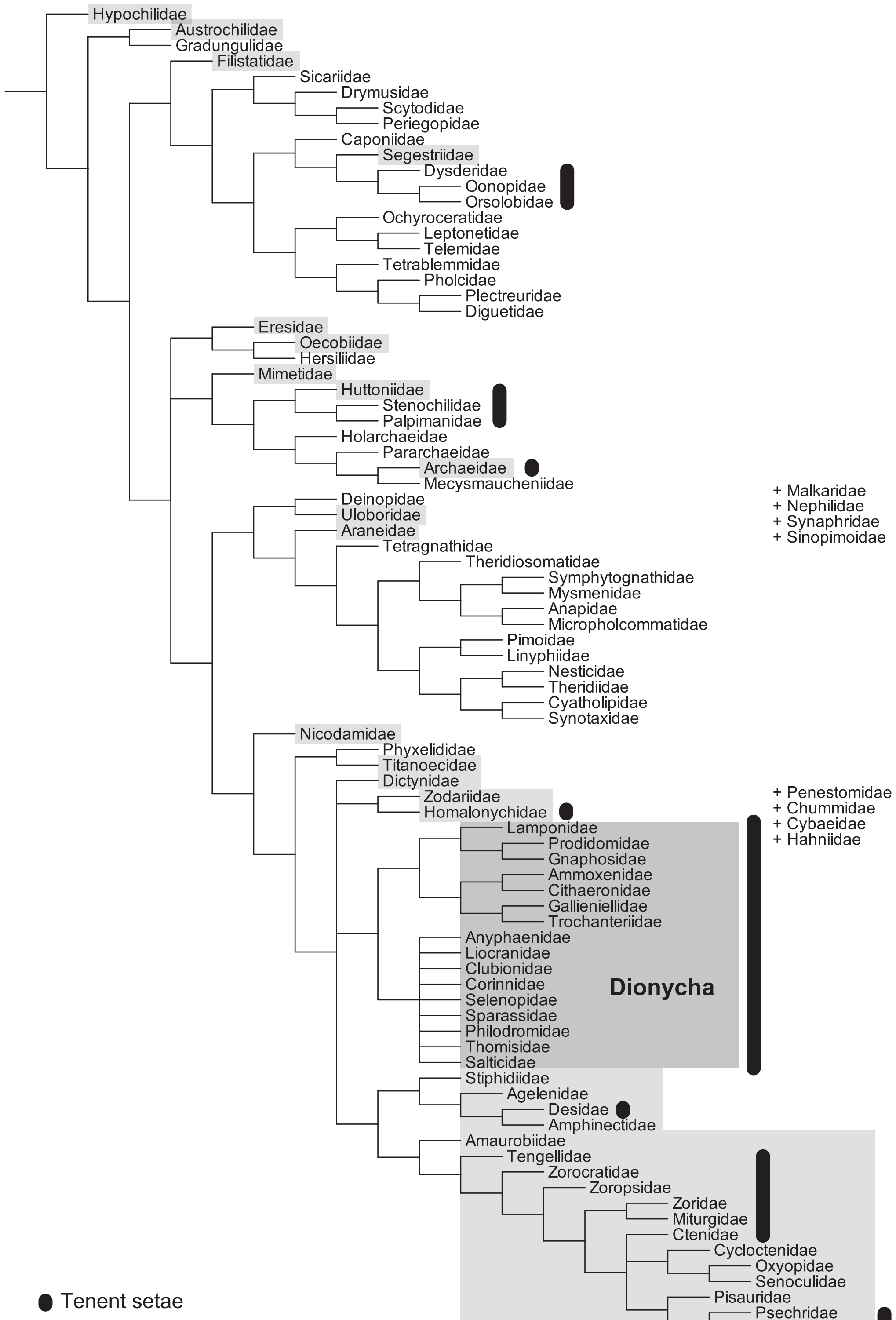

Hypochilidae
Austrochilidae
Gradungulidae
Filistatidae
Sicariidae
Drymusidae
Scytodidae
Periegopidae
Caponiidae
Segestriidae
Dysderidae
Oonopidae
Orsolobidae
Ochyroceratidae
Leptonetidae
Telemidae
Tetrablemmidae
Pholcidae
Plectreuridae
Diguetidae
Eresidae
Oecobiidae
Hersiliidae
Mimetidae
Huttoniidae
Stenochilidae
Palpimanidae
Holarchaeidae
Pararchaeidae
Archaeidae
Mecysmaucheniidae
Deinopidae
Uloboridae
Araneidae
Tetragnathidae
Theridiosomatidae
Symphytognathidae
Mysmenidae
Anapidae
Micropholcommatidae
Pimoidae
Linyphiidae
Nesticidae
Theridiidae
Cyatholipidae
Synotaxidae
+ Malkaridae
+ Nephilidae
+ Synaphridae
+ Sinopimoidae
Nicodamidae
Phyxelididae
Titanoecidae
Dictynidae
Zodariidae
Homalonychidae
Lamponidae
Prodidomidae
Gnaphosidae
Ammoxenidae
Cithaeronidae
Gallieniellidae
Trochanteriidae
Anyphaenidae
Liocranidae
Clubionidae
Corinnidae
Selenopidae
Sparassidae
Philodromidae
Thomisidae
Salticidae
Dionycha
+ Penestomidae
+ Chummidae
+ Cybaeidae
+ Hahniidae
Stiphidiidae
Agelenidae
Desidae
Amphinectidae
Amaurobiidae
Tengellidae
Zorocratidae
Zoropsidae
Zoridae
Miturgidae
Ctenidae
Cycloctenidae
Oxyopidae
Senoculidae
Pisauridae
Psechridae
Lycosidae
Trechaleidae
● Tenent setae

TABLE 9

Synapomorphies of the Divided Cribellum and RTA clades

See figure 188 for clades and table 11 for conventions.

RI	**Divided Cribellum clade, 181**
0.41	chilum [30]: absent → present
0.41	cheliceral boss [38]: absent → present
0.67	promargin cheliceral whisker setae [51]: absent → present at least one
0.60	promarginal escort seta [52]: absent → present
0.52	male palp retrolateral tibial apophysis [311]: absent → present
	RTA Clade, 185
0.40	carapace thoracic fovea shape [1]: wide depression → narrow dark longitudinal line
0.46	general metatarsal spination pattern [149]: leg III more than x-x-x or irregular → x-x-x
0.67	metatarsal trichobothria, number [187]: 1–2 → more than 2 any leg
0.82	tarsal trichobothria rows [190]: none → single row

RELATIONSHIPS OF OUTGROUPS

THE DIVIDED CRIBELLUM CLADE

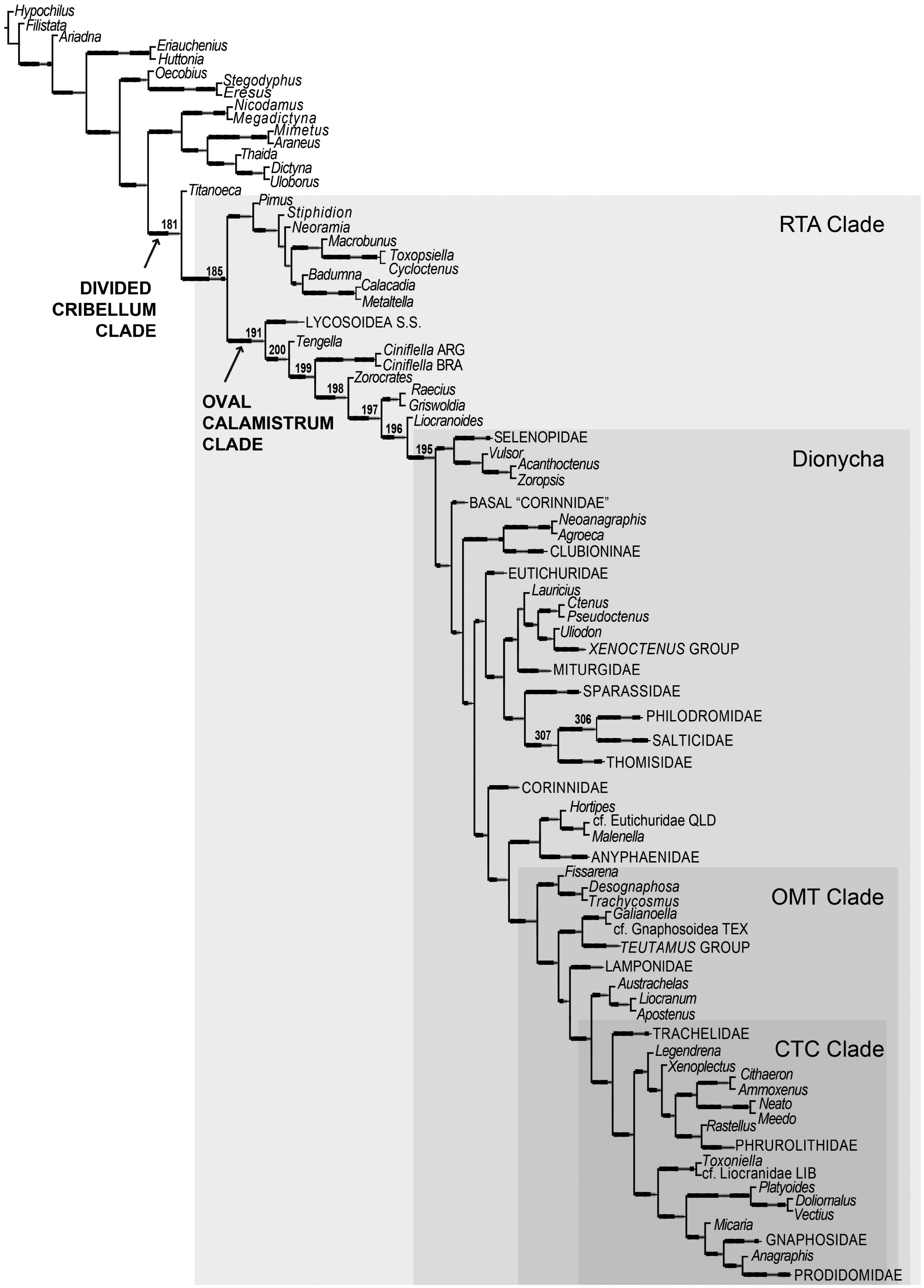
A clade compatible with the "Divided Cribellum clade" (fig. 188, table 9; Griswold et al., 1999, 2005) is recovered here, although with the divided cribellum optimized as plesiomorphic. In this dataset, the wild diversity in shapes and positions of processes on the male palpal tibia made it impossible to discriminate between a classically defined RTA, on the retrolateral-apical sector, and a process located on the dorsal-retrolateral-apical sector, as in titanoecids or dictynids. Several terminals well nested in the RTA clade have only one apophysis, mostly on the dorsal position, which are no doubt homologous with the RTA (e.g., *Elaver tigrinella*). The Divided Cribellum clade appears as well supported, although most of their putative synapomorphies usually also appear in *Thaida*, *Dictyna*, or *Uloborus* (here joined in a group by themselves). The RTA itself follows quite consistently the tree, although lost several times independently (fig. 191A). Most of the character changes on the basal branch of the Divided Cribellum clade are on the chelicerae and their articulation with the carapace (fig. 191B–E), probably associated with a closer engagement with prey, rather than the distant prey manipulation of the more definite web builders. The escort setae (char. 52) are rather homoplasious, but the more generalized line of whisker setae (char. 51) is a good candidate as a synapomorphy of this clade (fig. 191B, C).

THE RTA CLADE

This analysis recovers a robustly supported RTA clade (fig. 188, table 9). Even when the RTA is considered homologous with the process found in Titanoecidae, the RTA clade is well supported by a reorganization of the leg setae. The trichobothria extend to the tarsus, and there are multiple ones on the metatarsus. More notably, this group acquires a highly stereotyped disposition of leg macrosetae, where each individual spine can be homologized across a wide range of families (fig. 192). Together with the stronger chelicerae developed in the Divided Cribellum clade, the increase in trichobothria on the leg distal articles seems correlated with less dependency on webs to catch prey, toward more cursorial and active-hunter habits.

←

Fig. 187. Taxon sampling for the phylogenetic analysis, with families represented in this study shaded on an approximate summary hypotheses of araneomorph relationships at the time of starting this study (modified from Coddington et al., 2004, with changes from Ramírez, 2000; Platnick, 2002; Silva Davila, 2003; and Miller et al., 2010; at the right, eight families that were created or more precisely placed in subsequent contributions). Families including species with tenent setae, either from claw tuft or scopula, are marked with vertical black bars.


Hypochilus
Filistata
Ariadna
Eriauchenius
Huttonia
Oecobius
Stegodyphus
Eresus
Nicodamus
Megadictyna
Mimetus
Araneus
Thaida
Dictyna
Uloborus
Titanoeca
181
DIVIDED CRIBELLUM CLADE
185
Pimus
Stiphidion
Neoramia
Macrobunus
Toxopsiella
Cycloctenus
Badumna
Calacadia
Metaltella
RTA Clade
LYCOSOIDEA S.S.
191
200
Tengella
199
Ciniflella ARG
Ciniflella BRA
198
Zorocrates
197
Raecius
Griswoldia
196
Liocranoides
OVAL CALAMISTRUM CLADE
195
SELENOPIDAE
Vulsor
Acanthoctenus
Zoropsis
Dionycha
BASAL "CORINNIDAE"
Neoanagraphis
Agroeca
CLUBIONINAE
EUTICHURIDAE
Lauricius
Ctenus
Pseudoctenus
Uliodon
XENOCTENUS GROUP
MITURGIDAE
SPARASSIDAE
306
PHILODROMIDAE
SALTICIDAE
307
THOMISIDAE
CORINNIDAE
Hortipes
cf. Eutichuridae QLD
Malenella
ANYPHAENIDAE
Fissarena
Desognaphosa
Trachycosmus
OMT Clade
Galianoella
cf. Gnaphosoidea TEX
TEUTAMUS GROUP
LAMPONIDAE
Austrachelas
Liocranum
Apostenus
TRACHELIDAE
CTC Clade
Legendrena
Xenoplectus
Cithaeron
Ammoxenus
Neato
Meedo
Rastellus
PHRUROLITHIDAE
Toxoniella
cf. Liocranidae LIB
Platyoides
Doliomalus
Vectius
Micaria
GNAPHOSIDAE
Anagraphis
PRODIDOMIDAE

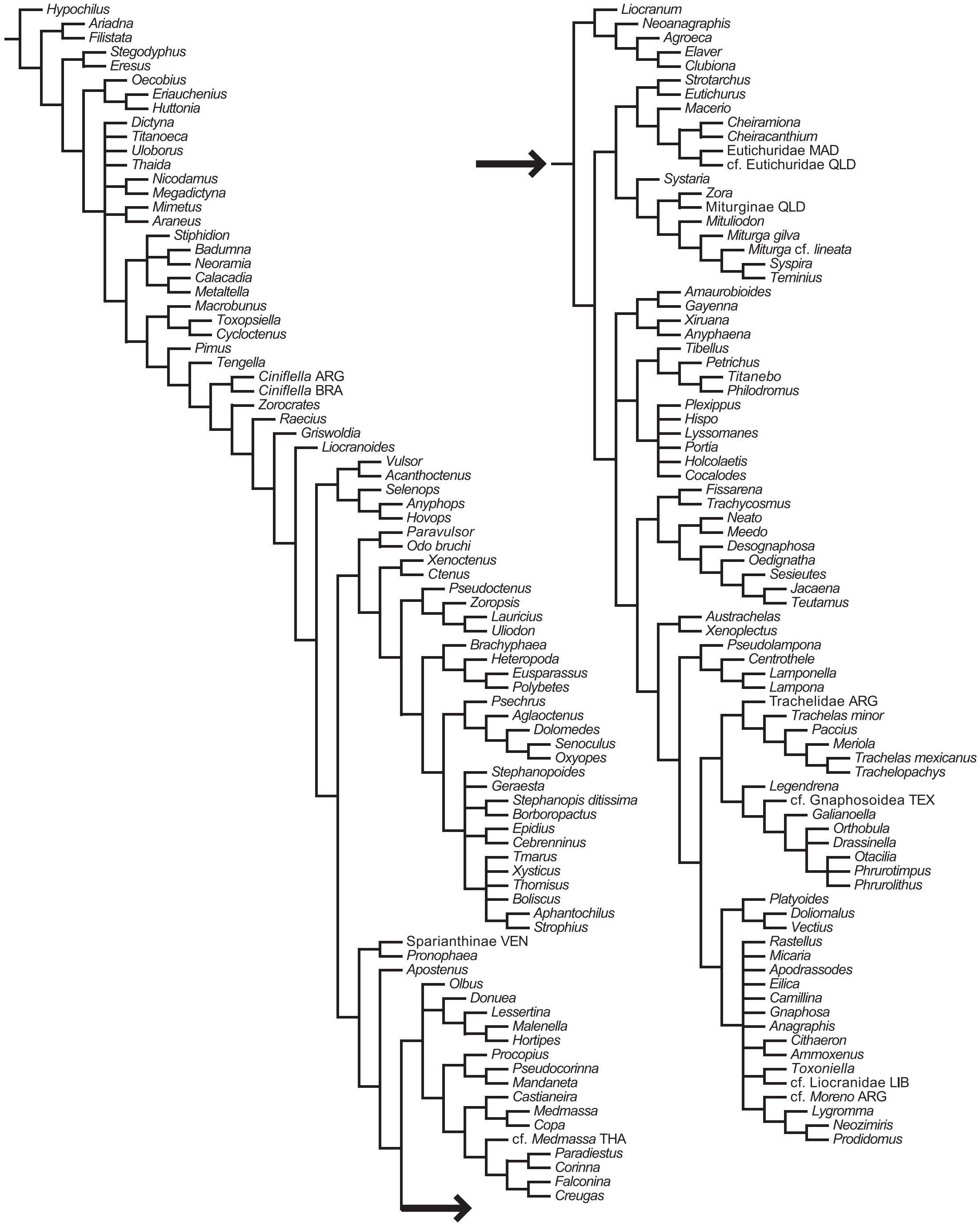

Hypochilus
Ariadna
Filistata
Stegodyphus
Eresus
Oecobius
Eriauchenius
Huttonia
Dictyna
Titanoeca
Uloborus
Thaida
Nicodamus
Megadictyna
Mimetus
Araneus
Stiphidion
Badumna
Neoramia
Calacadia
Metaltella
Macrobunus
Toxopsiella
Cycloctenus
Pimus
Tengella
Ciniflella ARG
Ciniflella BRA
Zorocrates
Raecius
Griswoldia
Liocranoides
Vulsor
Acanthoctenus
Selenops
Anyphops
Hovops
Paravulsor
Odo bruchi
Xenoctenus
Ctenus
Pseudoctenus
Zoropsis
Lauricius
Uliodon
Brachyphaea
Heteropoda
Eusparassus
Polybetes
Psechrus
Aglaoctenus
Dolomedes
Senoculus
Oxyopes
Stephanopoides
Geraesta
Stephanopis ditissima
Borboropactus
Epidius
Cebrenninus
Tmarus
Xysticus
Thomisus
Boliscus
Aphantochilus
Strophius
Sparianthinae VEN
Pronophaea
Apostenus
Olbus
Donuea
Lessertina
Malenella
Hortipes
Procopius
Pseudocorinna
Mandaneta
Castianeira
Medmassa
Copa
cf. Medmassa THA
Paradiestus
Corinna
Falconina
Creugas
Liocranum
Neoanagraphis
Agroeca
Elaver
Clubiona
Strotarchus
Eutichurus
Macerio
Cheiramiona
Cheiracanthium
Eutichuridae MAD
cf. Eutichuridae QLD
Systaria
Zora
Miturginae QLD
Mituliodon
Miturga gilva
Miturga cf. lineata
Syspira
Teminius
Amaurobioides
Gayenna
Xiruana
Anyphaena
Tibellus
Petrichus
Titanebo
Philodromus
Plexippus
Hispo
Lyssomanes
Portia
Holcolaetis
Cocalodes
Fissarena
Trachycosmus
Neato
Meedo
Desognaphosa
Oedignatha
Sesieutes
Jacaena
Teutamus
Austrachelas
Xenoplectus
Pseudolampona
Centrothele
Lamponella
Lampona
Trachelidae ARG
Trachelas minor
Paccius
Meriola
Trachelas mexicanus
Trachelopachys
Legendrena
cf. Gnaphosoidea TEX
Galianoella
Orthobula
Drassinella
Otacilia
Phrurotimpus
Phrurolithus
Platyoides
Doliomalus
Vectius
Rastellus
Micaria
Apodrassodes
Eilica
Camillina
Gnaphosa
Anagraphis
Cithaeron
Ammoxenus
Toxoniella
cf. Liocranidae LIB
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus

Fig. 189. Consensus of 1728 optimal trees under equal weights (length = 2923 steps).

←

Fig. 188. Cladogram summary of Dionycha and outgroups, obtained under implied weights (constant of concavity $k = 9$).

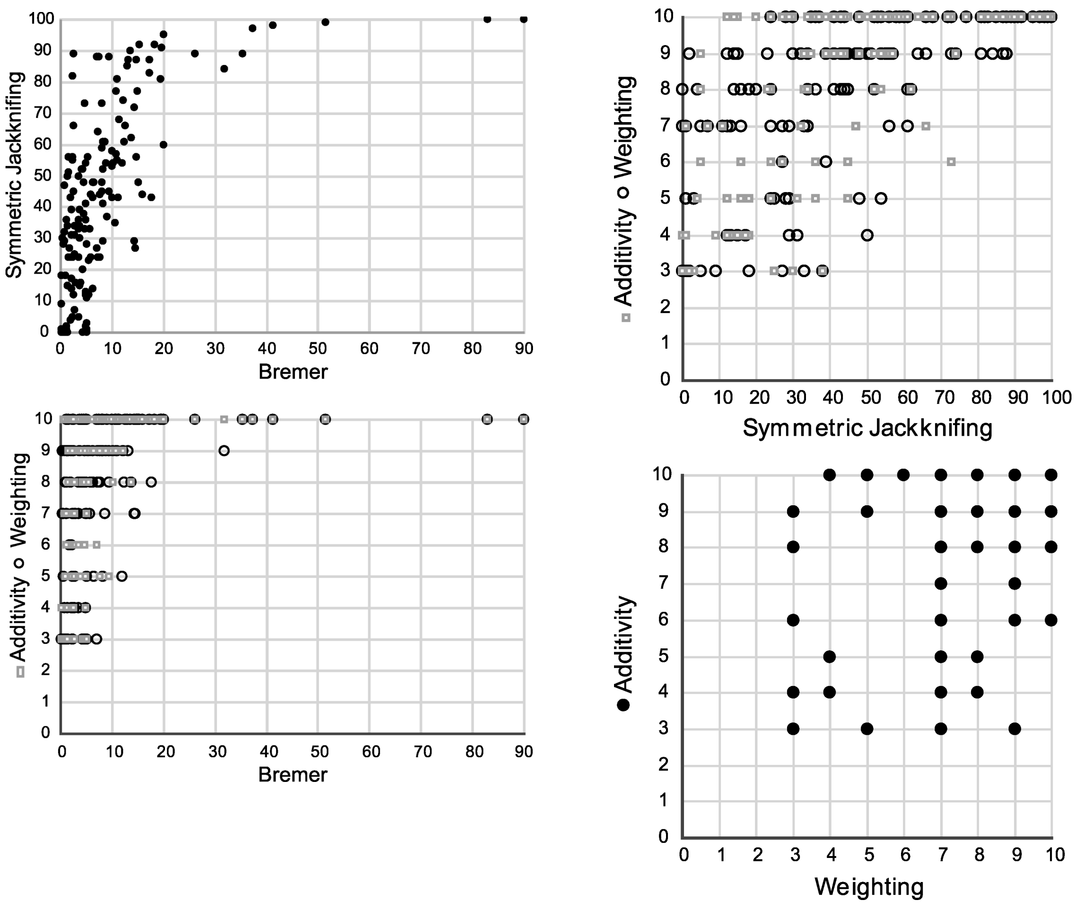


Fig. 190. Correlations between the measures of support and stability used in the phylogenetic analysis. Each point represents a clade. Additivity = number of character state ordering experiments (see table 3) where the clade is monophyletic. Weighting = number of character weighting regimes (see table 7) where the clade is monophyletic.

LYCOSOIDS AND THE ROOT OF DIONYCHA

All the cladistic analyses involving lycosoid spiders and their relatives produced considerably different resolutions for the higher grouping of families (Griswold, 1993; Griswold et al., 1999; Silva Davila, 2003; Griswold et al., 2005; Raven and Stumkat, 2005; see also Platnick and Ubick, 2007; Raven, 2012). The present analysis, by using a large sample of nonlycosoid families, has given further possibilities for alternative placements of putative lycosoid spiders. This analysis recovered one of the main clades, the Lycosoidea, s.s. (figs. 193A, 196B). As explained below, the overarching hypothesis for lycosoids and their kind, the oval calamistrum clade, is also recovered, but this time including the entire Dionycha lineage.

In this analysis the grate-shaped tapetum, a classical synapomorphy of lycosoids, appears convergently about five times (see below, and fig. 194A, B). Similarly, the locking lobes on the male copulatory bulb are quite homoplasious as well (fig. 194C, D). It is illustrative to explore the effect of a different taxon-sampling strategy using this dataset as a starting point, only considering in the analysis a subset of the terminals, following roughly the taxa sampled by Raven and Stumkat (2005). Such reduced dataset

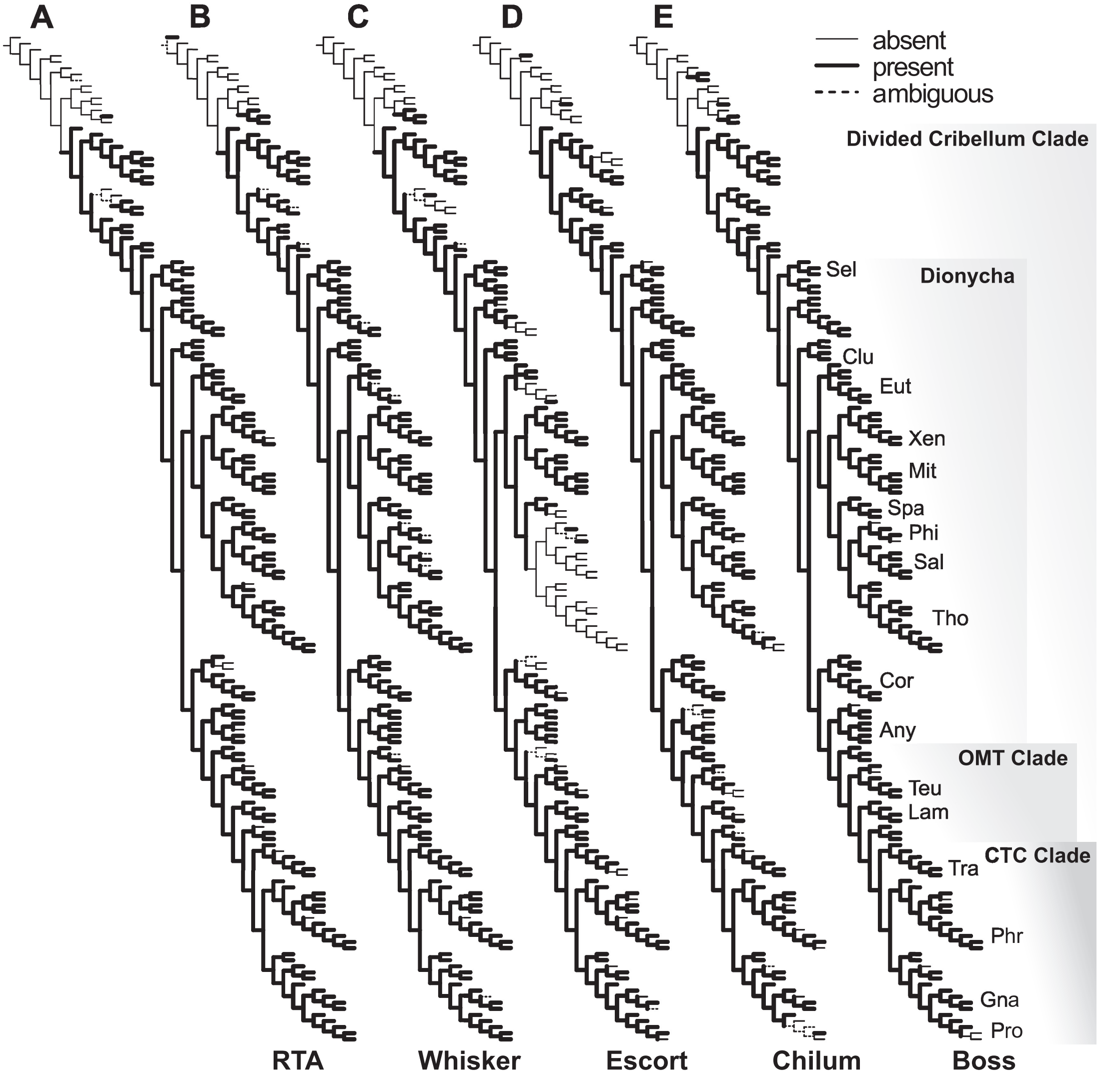

A
B
C
D
E
absent
present
ambiguous
Divided Cribellum Clade
Dionycha
OMT Clade
CTC Clade
Sel
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Cor
Any
Teu
Lam
Tra
Phr
Gna
Pro
RTA
Whisker
Escort
Chilum
Boss

Fig. 191. Mapping of characters marking the transition to the Divided Cribellum clade. **A.** Male palpal retrolateral tibia apophysis (RTA, char. 311). **B.** Cheliceral whisker setae (char. 51). **C.** Cheliceral escort setae (char. 52). **D.** Chilum (char. 30). **E.** Cheliceral boss (char. 38).

produces a tree (fig. 196A) with large differences from that obtained with more dionychan representatives, and also from the one selected by Raven and Stumkat (2005: fig. 2). This experiment illustrates how the inclusion of representatives of large groups that are considered, but not proved, to be unrelated (e.g., dionychans and the Austral Cribellate clade, see Miller et al., 2010) may have a profound impact on the resulting hypotheses.

THE OVAL CALAMISTRUM CLADE

The relationships of lycosoids and their kind might be unstable across analyses, but today it seems more firmly established that they arose within a clade where the calamistrum has changed its conformation, from two precisely aligned series of setae, to a rather disorganized patch, known as an "oval" calamistrum (Griswold, 1993; Griswold et

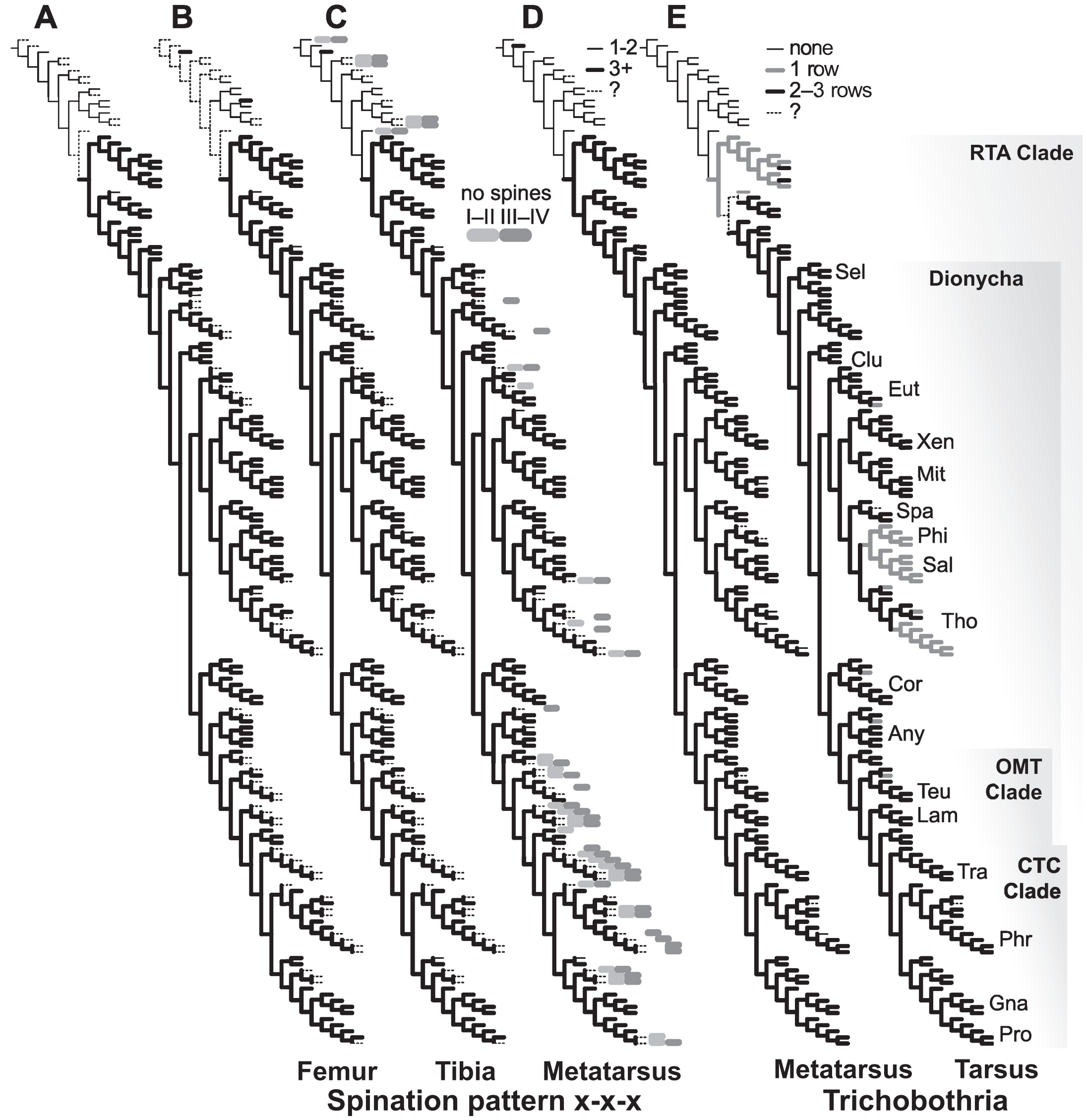

A
B
C
D
E
— 1-2
— 3+
--- ?
— none
— 1 row
— 2–3 rows
--- ?
no spines
I–II III–IV
RTA Clade
Dionycha
Sel
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Cor
Any
OMT Clade
Teu
Lam
CTC Clade
Tra
Phr
Gna
Pro
Femur
Tibia
Metatarsus
Spination pattern x-x-x
Metatarsus
Tarsus
Trichobothria

Fig. 192. Mapping of patterns of spines and trichobothria. A stereotyped pattern of macrosetae on femur, tibia, and metatarsi, placed in defined thirds, hence here named the "x-x-x" becomes established in the RTA clade, together with an increase of trichobothria on the distal leg articles. **A.** Femur (char. 147). **B.** Tibia (char. 148). **C.**Metatarsus (char. 149). **D.** Number of trichobothria on metatarsus (char. 187). **E.** Number of rows of trichobothria on tarsus (char. 190).

al., 1999; fig. 195). Such a change seems not to have implied associated transformations in morphology or behavior, as both the fine structure of the calamistral setae and the stereotyped movements used to card the silk bands remained the same as in their ancestors (see chars. 115, 387). The Oval Calamistrum clade is recovered here, but with an important change: Dionycha is deeply nested on it, and some taxa usually ascribed to lycosoids (zoropsids, ctenids, zorids, miturgids) appear mixed with dionychan lineages (fig. 188, tables 10, 11). Given the low support of the higher groups involving these lycosoidlike taxa, we should expect topological changes upon the addition of taxa and characters.

TABLE 10

Synapomorphies of the Oval Calamistrum clade and internal branches leading to Dionycha

See figure 190A for clades, and table 11 for conventions.

RI	**Oval Calamistrum Clade, 191**
1.00	calamistrum organization [110]: linear → oval
0.90	Sculpture on basal expansion of trichobothrial seta [184]: ridges or smooth → bumps
0.45	piriform spigot base cuticle texture [261]: concentric ridges → longitudinal ridges
	Lycosoidea, s.s., Clade 190—See table 12
	Clade 196
0.71	claw tuft [163]: absent → of tenent setae with widened tip
0.64	colulus [237]: well defined lobe → hairy plate or two setae
	Clade 197
(0.68)	patellar indentation I–II width [108]: wide → narrow
1.00	cribellar spigots grouping [232]: uniformly distributed → clumped
0.87	PLS modified spigot accompanying spigots [299]: modified spigot closely associated with accompanying spigots → not particularly associated with other spigots
	Clade 198
1.00	inferior tarsal claw I size [134]: large → small
0.53	PMS cylindrical gland spigots, number [283]: 2 → 3
	Clade 199
0.80	inferior tarsal claw teeth [135]: toothed → smooth
	Clade 200
0.40	internal prolongations on book lung cover [217]: absent → present
0.26	cuticular glands on epigyne [376]: absent → present
	Dionycha, Clade 195
1.00	inferior tarsal claw I size [134]: small → absent
(0.54)	epiandrous spigots [214]: absent → present
0.40	internal prolongations on book lung cover [217]: present → absent
(0.49)	embolus attachment [351]: fixed → flexibly attached
	Clade 301
0.50	male tibial crack [109]: absent → present
	***Ciniflella*, Clade 302**
0.80	calamistrum setae teeth lines [115]: one → two or more
0.37	metatarsal trichobothria rows [188]: single row → two or three rows
0.55	piriform spigots size sexual dimorphism [266]: about same size in male and female → male piriforms larger
0.50	female PMS minor ampullates, number [273]: two → one, no nubbin
0.34	female PMS aciniform spigots, number [276]: 4 or more → 2–3
0.25	male PMS aciniform spigots, number [277]: 4 or more → 2–3
0.44	RTA apical internal file [314]: absent → present

Some alternatives are explored here, such as the possibility that thomisids are derived lycosoids (fig. 215D). The conformation of the trichobothrial shaft base, covered by bumps (char. 184, RI = 0.90), offers a further synapomorphy for the Oval Calamistrum clade.

LYCOSOIDEA SENSU STRICTO: This analysis recovers a group coincident with the "true lycosoids" as resulted in Silva Davila (2003), although with different internal resolution (fig. 193B, table 12). The rest of the so-called lycosoids appear graded throughout the middle section of the tree, from *Tengella* (Tengellidae) to the classical dionychan families.

TENGELLIDAE, ZOROCRATIDAE, ZOROPSIDAE, AND CTENIDAE

TENGELLIDAE: The family Tengellidae currently includes cribellate and ecribellate spiders with three claws and a claw tuft (fig. 62D), or at least a group of tenent setae with intermediate morphology between a claw tuft and an advanced scopula (fig. 62C).

TABLE 11

Synapomorphies of some lycosoid groups

Weakly supported groups related with ctenids and miturgids, usually placed in Lycosoidea (see fig. 193B, C). Retention indices (RI) are reported for each character. Indices or clades in parentheses indicate that they are not preserved as synapomorphies or monophyletic groups, respectively, when branches of Bremer support ≤ 0.01 are collapsed.

RI	**Clade 201**
0.25	embolus prolateral furrow [353]: absent → present
	Clade 202
0.31	tarsal organ opening shape [127]: round to oval → teardrop or keyhole
0.37	metatarsal trichobothria rows [188]: single row → two or three rows
0.30	copulatory duct between primary and secondary spermathecae [377]: distinct → none confluent
	(Clade 203)
(0.44)	tegular (embolar base) locking lobe [342]: absent → present
(0.29)	secondary spermatheca size, relative to primary spermatheca [373]: smaller than primary spermatheca → about as large as primary spermatheca
	Clade 204
0.71	claw tuft insertion [173]: delimited plate separated by soft area from lateral cuticle → continuous with lateral cuticle
0.44	subtegular locking lobe [341]: absent → present
	Clade 210
0.50	serrula width [76]: wide bordering apex → very short
(0.71)	claw tuft insertion [173]: continuous with lateral cuticle → delimited plate separated by soft area from lateral cuticle
0.49	embolus attachment [351]: flexibly attached → fixed
	Clade 192
0.33	superior tarsal claws I teeth symmetry [139]: both claws similar → retroclaw many fewer teeth
0.54	epiandrous spigots [214]: present → absent
0.59	cribellum [229]: absent → present
0.64	colulus [237]: hairy plate or two setae → well defined lobe (includes cribellum)
0.50	ALS separation [243]: contiguous → separate about a diameter or more
0.42	major ampullates, number in male [258]: one plus nubbin → two
0.51	PLS modified spigot [296]: absent → present
	Clade 193
0.49	posterior eye row curvature [10]: approximately straight → notably recurved
0.36	male PMS minor ampullates, number [274]: one plus nubbin → two
0.35	cymbial retrobasal process [335]: absent → present
	Clade 194
0.50	apical ventral tarsal cuticle sclerotization [130]: entire sclerotized → unsclerotized transverse suture below claws
0.37	metatarsal trichobothria rows [188]: single row → two or three rows

So far no phylogenetic analysis produced a monophyletic Tengellidae, and the family lacks convincing diagnostic characters (see Silva Davila, 2003; Raven and Stumkat, 2003; Platnick and Ubick, 2007; Griswold et al., 2005). Similar to some proposed members of Lycosoidea, *Tengella* has an oval calamistrum and interlocking lobes on tegulum and subtegulum, but lacks the characteristic grate-shaped tapetum, the main reason to erect the superfamily. With such combination of characters, *Tengella* has been an obligate representative for cladistic analyses of lycosoids. This analysis includes several representatives of Tengellidae (fig. 197B, D–F). The type genus (*Tengella*), a representative of the *Liocranoides* complex (*Liocranoides*), a genus with uncertain relationships (*Lauricius*), and two species of the genus *Ciniflella*, a cribellate genus from Brazil and

TABLE 12
Synapomorphies of Lycosoidea sensu stricto and internal clades
See figure 196B for clades, and table 11 for conventions.

RI	**Lycosoidea, s.s., Clade 190**
0.49	posterior eye row curvature [10]: approximately straight → notably recurved
0.61	ALE tapetum type [22]: canoe → grate
0.63	PME tapetum type [25]: canoe → grate
0.53	PMS cylindrical gland spigots, number [283]: 2 → many
0.59	PLS cylindrical gland spigots, number [295]: 3 → 6 or more
0.40	lumen of secondary spermatheca [372]: secondary spermatheca a pore field without its own lumen → secondary spermatheca blind sac with defined lumen
	Clade 211
0.16	anterior eye row curvature [9]: approximately straight → notably recurved
0.84	metatarsus ventroapical end extension [118]: truncate or invaginated → extending below tarsus
0.43	scale axis flattened [158]: axis cylindrical → axis or entire scale flattened
0.50	female PMS minor ampullates, number [273]: two → one plus nubbin
0.80	minor ampullate on posterior median margin, posterior to the group of aciniforms [275]: absent → present
	Clade 212
0.67	retrocoxal hymen [102]: leg I → absent
0.59	male palp tibia ventral apical process [320]: absent or simple swelling or part of RTA → present
0.15	embolar basal process [352]: absent → present
0.76	prey-catching web [382]: present → absent
	Clade 213
0.68	patellar indentation I–II width [108]: wide → narrow
0.38	trichobothria proximal plate transversal ridges [178]: transversely ridged → smooth
0.59	cribellum [229]: present → absent
0.50	ALS separation [243]: separate about a diameter or more → contiguous
0.51	PLS modified spigot [296]: present → absent
0.29	secondary spermatheca size, relative to primary spermatheca [373]: smaller than primary spermatheca → about as large as primary spermatheca

northern Argentina that may be closely related to *Austrotengella* (both genera have similar copulatory bulbs and sculpture on the RTA; see Raven, 2012).

With this dataset, constraining Tengellidae (*Tengella*, *Lauricius*, and *Liocranoides*) as monophyletic is far suboptimal, without any synapomorphy for the group. Constraining a

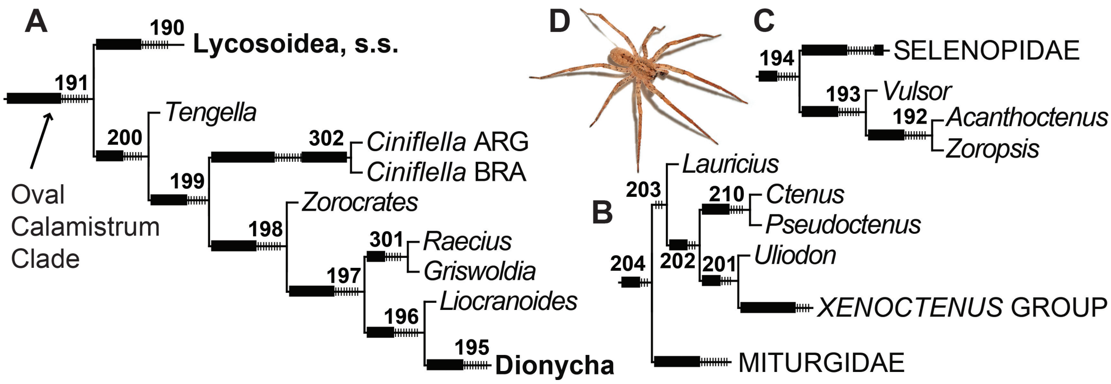

A
190
Lycosoidea, s.s.
191
Oval Calamistrum Clade
200
Tengella
199
302
Ciniflella ARG
Ciniflella BRA
198
Zorocrates
197
301
Raecius
Griswoldia
196
Liocranoides
195
Dionycha
D
C
194
SELENOPIDAE
193
Vulsor
192
Acanthoctenus
Zoropsis
B
203
Lauricius
210
Ctenus
Pseudoctenus
204
202
201
Uliodon
XENOCTENUS GROUP
MITURGIDAE

Fig. 193. **A.** Relationships of the Oval Calamistrum clade, and internal branches leading to Dionycha. **B, C.** Relationships of weakly supported groups related with ctenids and miturgids, formerly placed in Lycosoidea. **D.** *Zoropsis spinimana* (Zoropsidae; photo, Guido Gabriel).

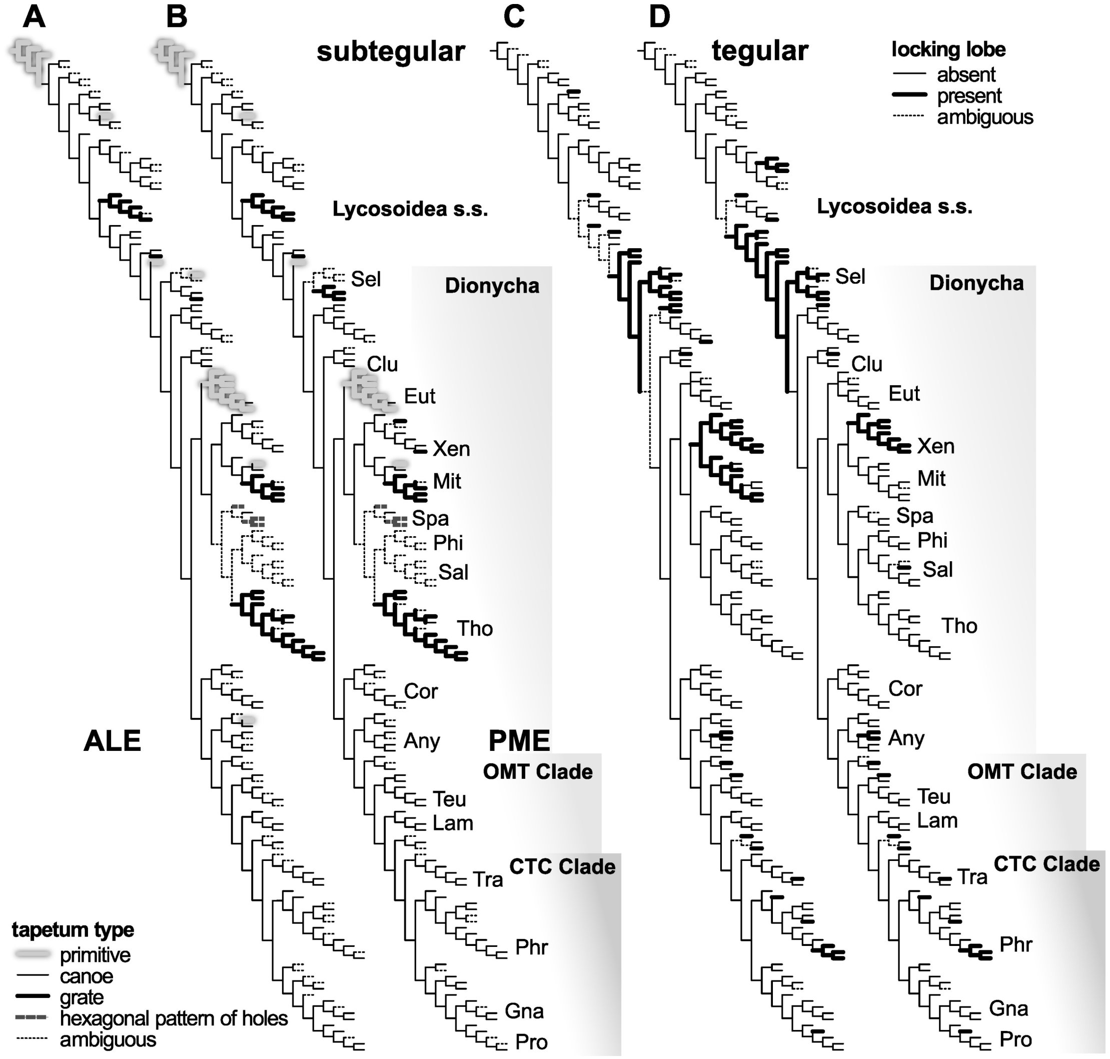

A
B
C
D
subtegular
tegular
locking lobe
absent
present
ambiguous
Lycosoidea s.s.
Lycosoidea s.s.
Sel
Dionycha
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Cor
Any
ALE
PME
OMT Clade
Teu
Lam
Tra
CTC Clade
Phr
Gna
Pro
Sel
Dionycha
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Cor
Any
OMT Clade
Teu
Lam
Tra
CTC Clade
Phr
Gna
Pro
tapetum type
primitive
canoe
grate
hexagonal pattern of holes
ambiguous

Fig. 194. Mapping of the tapetum of indirect eyes and locking lobes between tegulum and subtegulum. **A.** ALE tapetum (char. 22). **B.** PME tapetum (char. 25). **C.** Tegular lobe (char. 341). **D.** Subtegular lobe (char. 342).

larger group, including *Ciniflella*, produced similar results. A member of the *Liocranoides* complex, with three claws and well-delimited claw tufts, is a mandatory representative in this analysis of Dionycha, and turned out to be a good candidate for the root of Dionycha (see below).

ZOROCRATIDAE: This dataset includes *Zorocrates* (fig. 197A) and *Raecius* as two representatives of Zorocratidae (or Zorocratinae, Raven and Stumkat, 2005). When they are constrained to be sister groups, the only synapomorphy is the presence of an embolar basal process (char. 352), a highly homoplasious character (RI = 0.15).

CTENIDAE AND ZOROPSIDAE: This analysis has failed to recover a monophyletic Ctenidae (here represented by *Ctenus*, *Vulsor*, and the cribellate *Acanthoctenus*). The same failure was also depicted by Griswold (1993), Bosselaers (2002), and Raven and Stumkat (2005). The grouping of *Acanthoctenus* with *Zoropsis* (Zoropsidae) is indeed classic and traces back to Simon (1892; see Silva Davila,

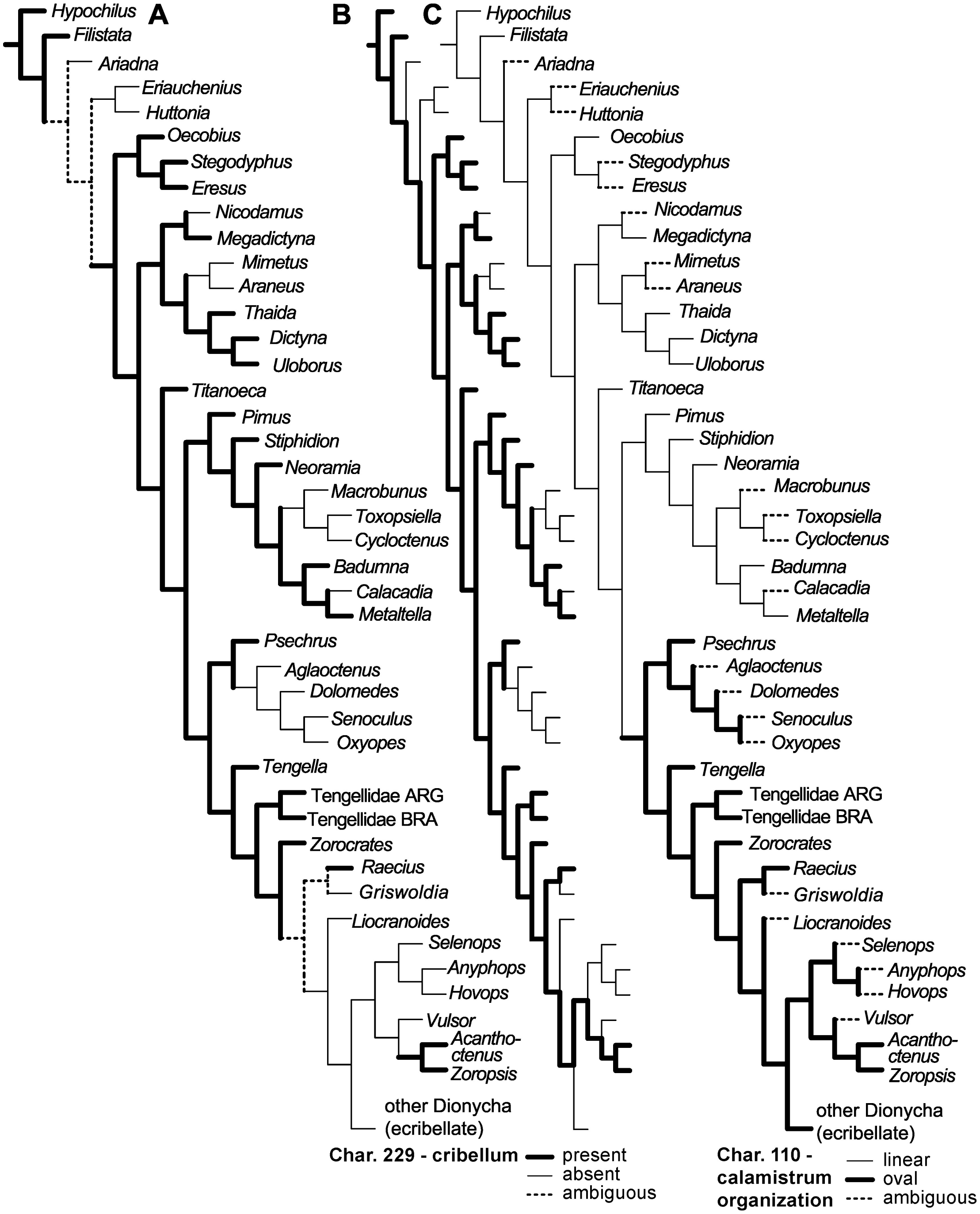

A
B
C
Hypochilus
Filistata
Ariadna
Eriauchenius
Huttonia
Oecobius
Stegodyphus
Eresus
Nicodamus
Megadictyna
Mimetus
Araneus
Thaida
Dictyna
Uloborus
Titanoeca
Pimus
Stiphidion
Neoramia
Macrobunus
Toxopsiella
Cycloctenus
Badumna
Calacadia
Metaltella
Psechrus
Aglaoctenus
Dolomedes
Senoculus
Oxyopes
Tengella
Tengellidae ARG
Tengellidae BRA
Zorocrates
Raecius
Griswoldia
Liocranoides
Selenops
Anyphops
Hovops
Vulsor
Acanthoctenus
Zoropsis
other Dionycha (ecribellate)
Char. 229 - cribellum
present
absent
ambiguous
Char. 110 - calamistrum organization
linear
oval
ambiguous

Fig. 195. Mapping of the cribellum and types of calamistrum. **A.** The optimization with equal costs implies at least one regain of the cribellum in *Acanthoctenus* + *Zoropsis*, with nine independent losses. **B.** Mapping under autoweighted optimization, which accumulates the homoplasy on the already homoplasious losses; this optimization implies a primitive cribellum and 12 independent losses. **C.** Dionycha arises from a clade with oval calamistrum.

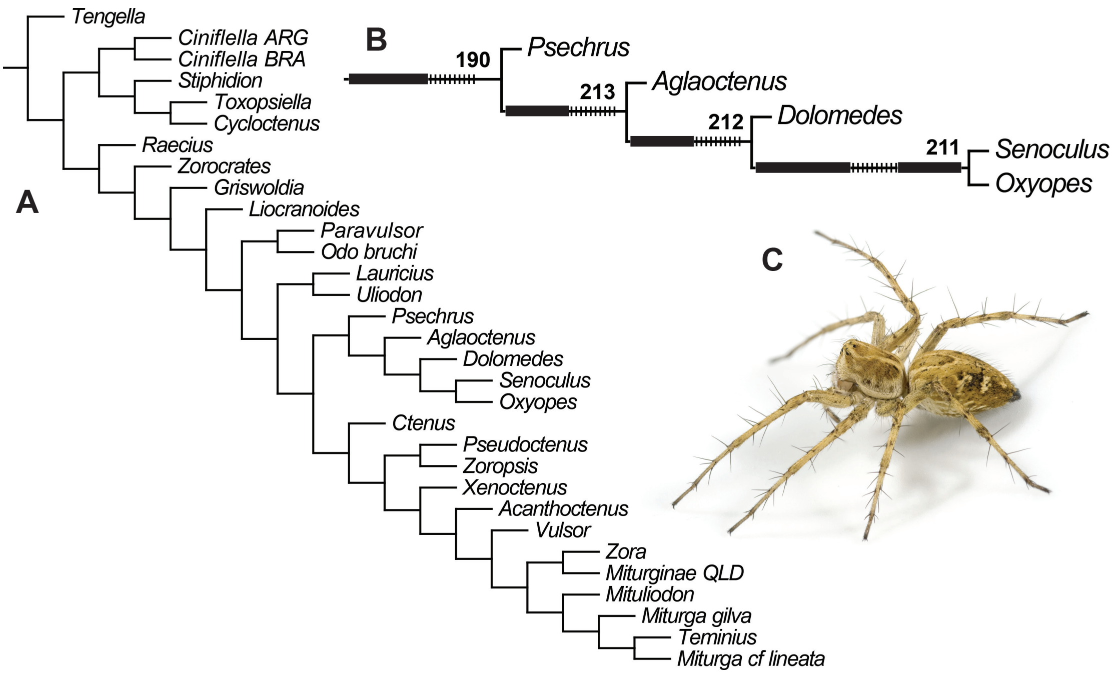

A
Tengella
Ciniflella ARG
Ciniflella BRA
Stiphidion
Toxopsiella
Cycloctenus
Raecius
Zorocrates
Griswoldia
Liocranoides
Paravulsor
Odo bruchi
Lauricius
Uliodon
Psechrus
Aglaoctenus
Dolomedes
Senoculus
Oxyopes
Ctenus
Pseudoctenus
Zoropsis
Xenoctenus
Acanthoctenus
Vulsor
Zora
Miturginae QLD
Mituliodon
Miturga gilva
Teminius
Miturga cf lineata
B
190
Psechrus
213
Aglaoctenus
212
Dolomedes
211
Senoculus
Oxyopes
C

Fig. 196. **A.** Results from a reduced dataset including only classical lycosoid representatives, following a sampling strategy similarly as in Raven and Stumkat (2005). **B.** Cladogram of Lycosoidea s.s., from this study. **C.** *Oxyopes heterophthalmus* (Oxyopidae; photo, Arno Grabolle).

2003, for discussion), and is obtained in other analyses with few representatives of lycosoids (Griswold et al., 1999, 2005; see also Griswold, 1993 and Bosselaers, 2002 for similar results). Silva Davila (2003: 29) considered such a group as an alternative resolution with a single origin of the cribellum, but yet unsupported by any synapomorphy. The group *Acanthoctenus* + *Zoropsis* is obtained here (clade 192), but the synapomorphies are still unconvincing, mostly related to the reversal to primitive configurations of the spinning organs, including the regaining of a cribellum (fig. 195, see below), the space between ALS to accommodate it, and the modified PLS spigots. In a recent analysis, Polotow and Brescovit (2010) found support for the placement of *Acanthoctenus* in Ctenidae, although this time with two regains of the cribellum.

A constrained analysis forcing Zoropsidae (as *Zoropsis* + *Uliodon* + *Pseudoctenus* + *Griswoldia*) to be monophyletic would be preferable to one that includes *Zorocrates* and *Raecius* as well, as in Raven and Stumkat (2005) (FD = 16.73 and C/F = 1.34, vs. FD = 39.45 and C/F = 1.93). In both cases the group would be supported by the short, wide cymbium, not extending beyond the copulatory bulb (char. 325).

When the family Ctenidae is constrained as monophyletic, including *Acanthoctenus*, the results are slightly suboptimal, with considerable gain in other characters (FD = 5.65 and C/F = 1.18), mainly from the eyes. With that resolution Ctenidae would be supported by the recurved anterior eye row (char. 9) and the reduced black cup of ALE (char. 16).

THE EVOLUTION OF THE CRIBELLUM AND CALAMISTRUM: As it is usual with higher-level analyses involving several cribellate and ecribellate representatives, in this analysis a standard reconstruction of the evolution of the cribellum involves at least one resurrection of the cribellum from a group that has lost it (fig. 195). The explanation of this effect is simple. The optimization of the cribellum is ambiguous, and implies nine losses and one regain of the cribellum, in one extreme, to seven losses and

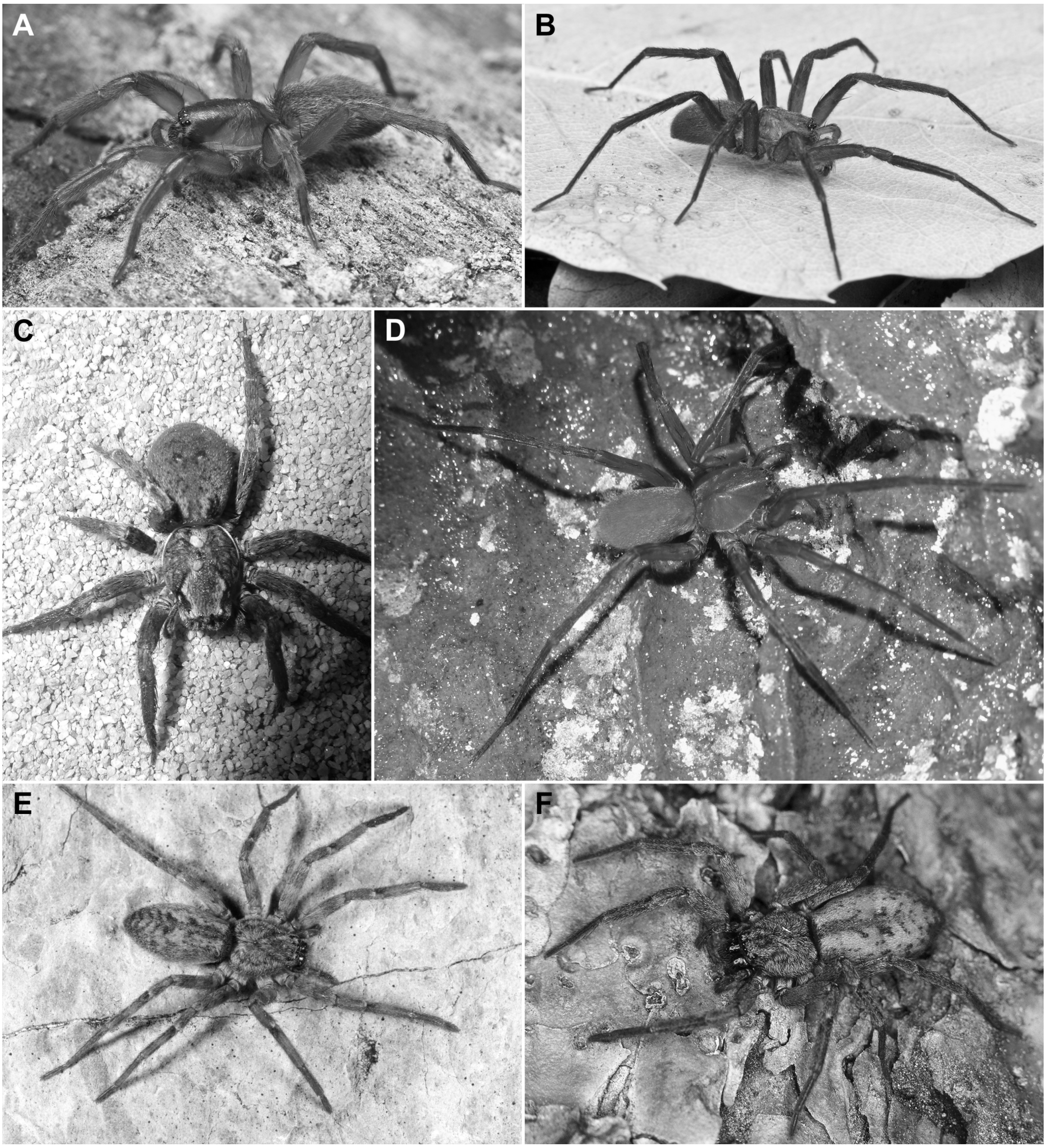


Fig. 197. Representatives of families usually ascribed to Lycosoidea, habitus. **A.** *Zorocrates aemulus* female (Zorocratidae; photo, Marshal Hedin). **B.** *Socalchemmis idyllwild* male (Tengellidae; photo, Marshal Hedin). **C.** *Kilyana hendersoni* female (Zoropsidae; photo, Robert Raven). **D.** *Liocranoides* sp. female (Tengellidae; photo, Alan Cressler). **E.** *Lauricius hooki* female (photo, Jillian Cowles). **F.** Same (photo, David Richman, New Mexico State University).

three regains, in the other. The cribellum has been lost so many times in so many disparate groups that any sampling of representatives is likely to imply some reacquisition of the cribellum, even if the relationships were correctly estimated. An exception is the analysis of Griswold et al. (2005), which was purposely biased toward the sampling of cribellate taxa as a proxy for the more primitive representatives of the higher groups, hence diminishing the sampled instances of cribellum losses.

An alternative representation of the evolution of the cribellum may take into account the high frequency of cribellum losses relative to regains, and produce reconstructions where the losses are more likely than the gains. In the analysis of entelegynes of Miller et al. (2010), a Bayesian analysis with a rate of losses more than twice the rate of gains was sufficient to obtain a single origin of the cribellum (primitively present with 15 losses, vs. 8 gains and 5 losses under equal rates). This can be modeled as well with asymmetric transformation costs, extending the idea of implied weighting using homoplasy to the transformations between states, using auto-weighted optimization (Goloboff, 1997). Optimizing the cribellum character in this dataset and the preferred tree under such regime results in a primitive cribellum and 12 independent losses, in a range of strong to mild concavities (*k* from 1 to 11).

THE ROOT OF DIONYCHA AND THE EVOLUTION OF THE CLAW TUFT

In this analysis a large dionychan clade gets connected to an internal branch of the Oval Calamistrum clade. *Liocranoides*, at clade 195, marks the appearance of the dionychan claw tuft, at the end of a grade with reduced inferior claw, well correlated with the appearance of the claw tuft (fig. 198A, B). At clade 194 the inferior claw is lost, to give rise to Dionycha (clade 195, fig. 188).

The loss of the third tarsal claw and the appearance of claw tufts is a common syndrome that has evolved repeatedly in distantly related spider groups with some kind of wandering life style, from mygalomorphs to haplogynes and palpimanoids, and the families treated here. As anticipated in the Introduction, the taxonomic distribution of tenent setae (fig. 187) indicates from the start that we should expect high homoplasy in that character system. A closer examination of the setae making the claw tufts reveals that their fine morphology is remarkably similar: the sector making contact with the surface is a flat widened area uniformly lined with thin flexible barbs with flat expanded tips (figs. 85C, 90F). This convergence would be extremely curious, but it was also invented many other times, in multiple insect orders, and even lizards have twice developed a remarkably similar morphology (Arzt et al., 2003; Beutel and Gorb, 2001; Filipov et al., 2011; Gorb, 2008). The basic functional principle is that the barbs, and especially their tips are flexible, maximizing contact with irregular surfaces; the multiple contact points produce molecular Van der Waals forces able to support the spider's weight.

As expected, the two characters coding the presence of tarsal scopula and claw tuft have lots of homoplasy (23 steps, CI = 0.04, and 21 steps, CI = 0.09, respectively), but still retain good phylogenetic signal (RI = 0.67 and 0.71). This study presents many kinds of morphological variation in tenent setae scored as characters, beyond the mere presence of a tenent surface. Of the 65 characters about setae in general, the 15 from tenent setae show much higher consistency and retention indices (table 8), and define higher level clades, such as Sparassidae, Philodromidae and the Claw Tuft Clasper (CTC) clade, to name just a few. The discovery of tenent pads in the tip of macrosetae (char. 155), and the occasional occurrence of thick, erect scopular setae reminiscent of macrosetae (Ubick and Platnick, 1991) suggest that the signaling pathway establishing the identity of the setal types may overpass their usual boundaries, probably recruiting scopular setae to develop as macrosetae.

The pseudotenent setae, which are morphologically intermediate between hairs and tenent setae, are not intermediate in phylogeny, but derived from tenent setae (fig. 198B); the optimization on the tree suggests only one instance of transformation from pseudotenent to tenent, in the thomisid *Aphantochilus*. The insertion of the claw tuft on a delimited plate has been lost and gained multiple times in this tree (fig. 198C), notably in the the Claw Tuft Clasper (CTC) clade, which have developed a novel mechanism to move the claw tuft, alternative to the hydraulic movement allowed by a separate claw tuft plate (see The Claw Tuft Clasper (CTC) Clade below). Other groups with claw tufts inserted on continuous cuticle are the anyphaenids, with

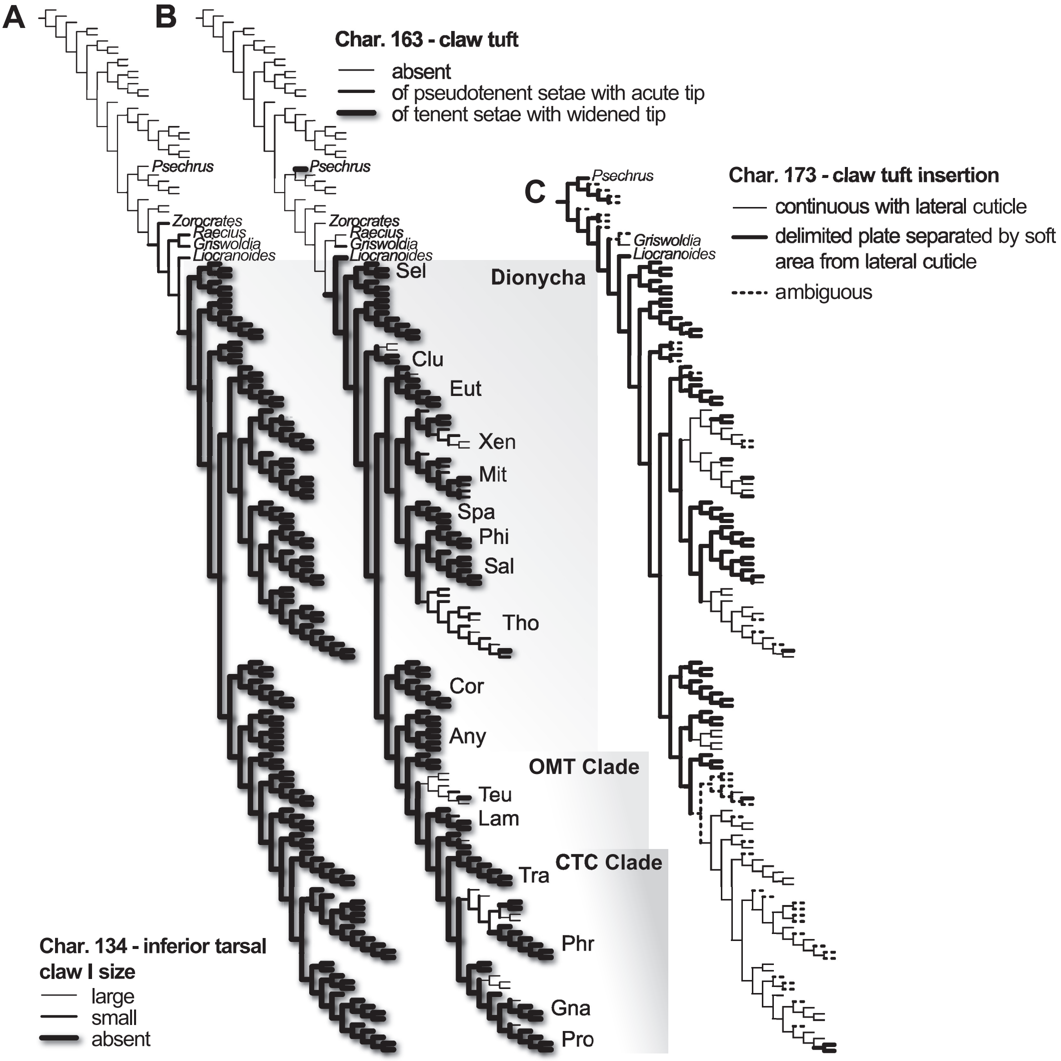

A
B
C
Char. 163 - claw tuft
absent
of pseudotenent setae with acute tip
of tenent setae with widened tip
Char. 173 - claw tuft insertion
continuous with lateral cuticle
delimited plate separated by soft area from lateral cuticle
ambiguous
Char. 134 - inferior tarsal claw I size
large
small
absent
Psechrus
Zorocrates
Raecius
Griswoldia
Liocranoides
Sel
Dionycha
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Cor
Any
OMT Clade
Teu
Lam
Tra
CTC Clade
Phr
Gna
Pro

Fig. 198. Mapping of the inferior tarsal claw and the claw tuft setae. **A.** The loss of the inferior tarsal claw is here reconstructed as arising from a grade with reduced claw. **B.** *Aphantochilus* is the only case where the tenent setae seem derived from a pseudotenent conformation. **C.** The separate plate for the claw tuft has been lost and aquired multiple times.

widened tenent setae, and also several miturgids and thomisids with pseudotenent setae. This study indicates that the disctinction made in mygalomorphs by Raven (1986) of true claw tufts, inserted on separate pads, and false claw tufts, interpreted as an extended scopula, does not describe well the morphology found in dionychan spiders, especially in the CTC clade and in anyphaenids, where the claw tuft is fully functional and provided with distinctly specialized tenent setae, but yet the claw tuft is inserted on continuous cuticle.

PRECOXAL TRIANGLES AND "ANYPHAENOIDEA": This dataset is useful to test and illustrate Penniman's (1985) idea of "Anyphaenoidea," defined by the presence of precoxal triangles (char. 95), including Anyphaenidae, Clubionidae, Gnaphosidae, Corinnidae and Phrurolithinae. As seen in the optimization (fig. 199A), the precoxal trian-

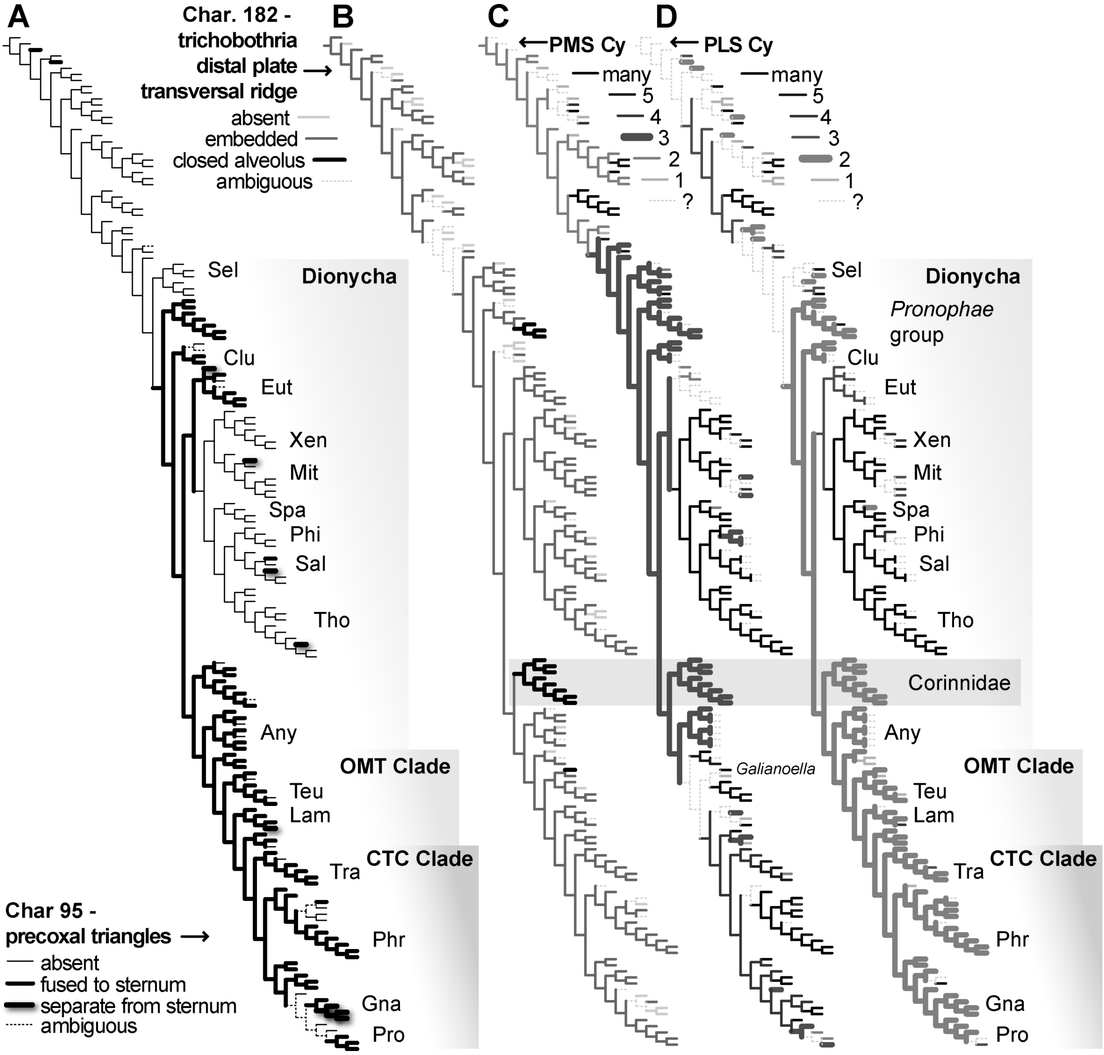

A
Char. 182 -
trichobothria
distal plate
transversal ridge
absent
embedded
closed alveolus
ambiguous
B
C
PMS Cy
many
5
4
3
2
1
?
D
PLS Cy
many
5
4
3
2
1
?
Sel
Dionycha
Pronophae
group
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Corinnidae
Any
OMT Clade
Galianoella
Teu
Lam
Tra
CTC Clade
Phr
Gna
Pro
Char 95 -
precoxal triangles
absent
fused to sternum
separate from sternum
ambiguous

Fig. 199. **A.** Mapping of the precoxal triangles (char. 95). **B–D.** Optimization of characters that were proposed as putative synapomorphies of Corinnidae. **B.** The closed alveolus of trichobothria (char. 182, state 2) is a synapomorphy of Corinnidae, with homoplasy in the *Pronophaea* group and in *Galianoella* (Gallieniellidae). **C, D.** The configuration of three cylindrical gland spigots on PMS and two on PLS is common in many families.

gles are consistently found in those groups, although they have been lost several times. A constrained analysis forcing the main clades with precoxal triangles as a monophyletic group would have such a group supported only by the triangles themselves, plus an undivided chilum configuration (char. 31, extremely homoplasious), and it would be suboptimal and without much gain from other characters (FD = 30.85, C/F = 3.48).

MAIN CLADES OF DIONYCHA

The results presented here are somehow disappointing by not finding strong support for the relationships of the basal relationships within Dionycha, but are also optimistic as regards new hypotheses, such as the splitting of the former Corinnidae into distinct families, and the recognition of the Oblique Median Tapetum (OMT) and CTC clades,

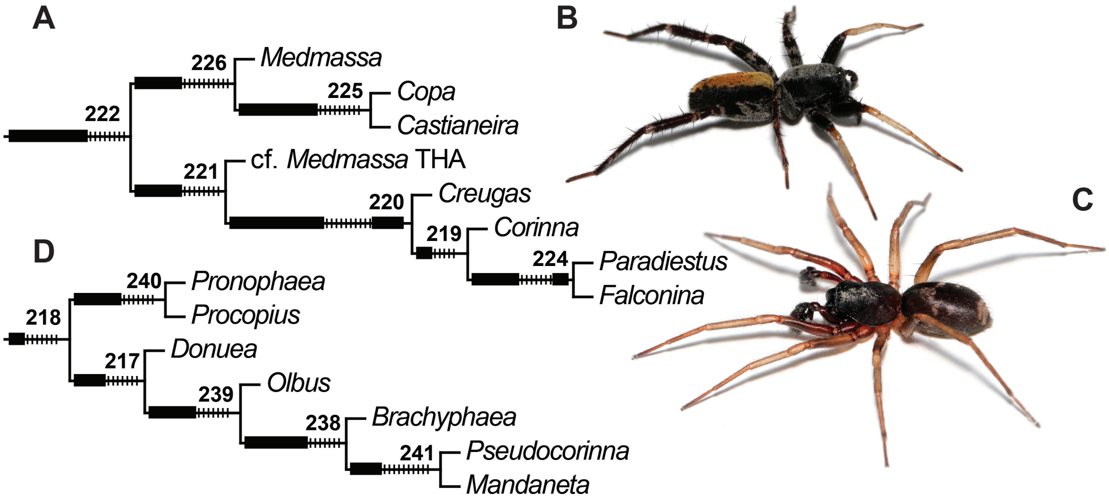


Fig. 200. **A.** Cladogram of Corinnidae s.s. **B.** *Castianeira descripta* female (Castianeirinae; photo, Joseph T. Lapp). **C.** *Falconina gracilis* male (Corinninae; photo, Joseph T. Lapp). **D.** Cladogram of the *Pronophaea* group.

including the gnaphosoids and their kin. The example case of the relationships of selenopids explained below is illustrative of how a small change in the interpretation of a few cells in the dataset produces significant rearrangements on the tree. The following sections will not devote much space to discussing regions of the tree with low support and sensitive to weighting regimes, as it is clear that these will change upon the addition of new taxa and sources of data.

CORINNIDAE AND ALLIES

Corinnidae is here retrieved in a restricted sense, including only the subfamilies Corinninae and Castianeirinae (figs. 200, 201A–D). Both groups are united by a particular conformation of the trichobothrial socket, with the proximal plate distal ridge joining in a closed alveolus (char. 182 state 2; fig. 199B; see table 13). Other characters supporting such a grouping are the loss of a median apophysis and the epigynal lobes fused in a common plate (chars. 356, 365). Classical corinnines are supported by the sperm duct making a particular spiralling (char. 348) and with a distal thickness (char. 346) (Bonaldo, 2000). The genus cf. *Medmassa* THA appears as the sister group of Corinninae, and may be a representative of a larger Old World clade of true Corinnidae including the African *Corinna natalis* as well (see Haddad, 2005).

Bonaldo (1997) and Ramírez et al. (2001) had set apart a group of putative corinnid genera retaining the median apophysis in the male copulatory bulb. Two characters invoked to affiliate those genera as corinnids are the lowered distal plate of the trichobothria, below a transverse ridge (char. 182 state 1) and a particular configuration of large cylindrical gland spigots (three on PMS, two on PLS; Penniman, 1985: fig. 32) (see fig. 199B–D). The trichobothrial character turned out to be very homoplasious, plagued with intermediate conditions, and hard to define; a transverse ridge is widespread through most families in this dataset. A more restricted condition (the closed alveolus, state 2) is homoplasious as well, but still defines some groups. The configuration of cylindrical gland spigots is common in other groups as well. This dataset includes several representatives of those putative corinnids (*Pronophaea*, *Procopius*, *Olbus*, *Pseudocorinna*, *Mandaneta*; fig. 201E–G). In this analysis those representatives ended up clustering together in what is here called the *Pronophaea* group (clade 218, table 14), but only in a range of weighting parameters and with weak support.

TABLE 13
Synapomorphies of Corinnidae and internal clades
See figure 200A for clades, and table 11 for conventions.

RI	**Corinnidae, Clade 222**
(0.67)	tarsal cuticle texture [100]: fingerprint → smooth
0.32	trichobothria distal plate transverse ridge [182]: distal plate embedded below transverse ridge → distal ridge continuous in a closed alveolus
0.60	dorsal scutum on male abdomen [205]: absent → present
0.49	embolus attachment [351]: flexibly attached → fixed
0.48	median apophysis [356]: present → absent
0.49	epigynum lobes [365]: lateral lobe and median field delimited by furrows or sutures → undivided plate suture not visible
	Corinninae, Clade 220
0.42	major ampullates, number in male [258]: one plus nubbin → two
(0.36)	male PMS minor ampullates, number [274]: one plus nubbin → two
0.75	sperm duct distal thickness [346]: gradually tapering, or thinned before embolus → thick sclerotized apical bulb
1.00	sperm duct spiral meander in ventral tegulum [348]: absent → present
(0.26)	cuticular glands on epigyne [376]: absent → present
	Clade 219
(0.71)	epiandrous spigots disposition [215]: two definite bunches → dispersed
	Clade 224
0.50	aciniform spigot shaft barbs [279]: only shallow sculpture or smooth → well defined barbs
	Clade 221
0.43	scale axis flattened [158]: axis cylindrical → axis or entire scale flattened
0.44	male epigastric sclerite [207]: absent → present
0.35	cymbial retrobasal process [335]: absent → present
	Castianeirinae, Clade 226
0.44	cymbial tip ventral groove [323]: absent → present
0.55	cymbium dorsal chemosensory patch [324]: present → absent
0.40	lumen of secondary spermatheca [372]: secondary spermatheca blind sac with defined lumen → secondary spermatheca a pore field without its own lumen
	Clade 225
0.22	dorsal scutum on female abdomen [201]: absent → present
0.52	male palp retrolateral tibial apophysis [311]: present → absent
0.50	embolus screw shaped [354]: absent → present

At any rate, there is not much evidence suggesting that they are closely related with true corinnids. The obtained tree includes as well two very dissimilar genera: the Malagasy *Donuea*, today placed in Liocranidae (Bosselaers et al., 2010), lacks cylindrical gland spigots; the African *Brachyphaea*, usually listed in Trachelinae, lacks a median apophysis. This grouping is rather unconvincing, but those genera lack the synapomorphies of clubionids (the modified male ALS) or trachelines (the characteristic claw tuft setae). Note that the genus *Oedignatha*, also a litter dweller with heavily sclerotized body similar to several members of the *Pronophaea* group, is here placed at a distance, in the OMT clade. However, a constrained analysis forcing *Oedignatha* within the *Pronophaea* group recovers signals from many other characters as well (FD = 16.19, C/F = 1.19).

THE LIMITS OF CLUBIONIDS, MITURGIDS, AND EUTICHURIDS

Lehtinen erected Miturgidae as a large, provisional assemblage of groups, and admitted that they may probably be considered separate families in the near future (1967: 314, 315; see Bonaldo et al., 2012). Time proved him right, as his former miturgids are now members of Tengellidae, Zoropsidae, Zorocratidae, and Anyphaenidae, to name

TABLE 14
Synapomorphies of the *Pronophaea* group and internal clades
See figure 200D for clades, and table 11 for conventions.

RI	***Pronophaea* group, Clade 218**
(0.67)	tarsal cuticle texture [100]: fingerprint → smooth
(0.48)	trochanter distal ventral margin notch [105]: deep at least legs I–II → shallow or absent
(0.55)	scales [157]: present → absent
	Clade 217
(0.71)	epiandrous spigots disposition [215]: two definite bunches → dispersed
	Clade 238
0.60	promarginal escort seta [52]: present → absent
0.32	trichobothria distal plate transverse ridge [182]: distal plate embedded below transverse ridge → distal ridge continuous in a closed alveolus
0.37	metatarsal trichobothria rows [188]: single row → two or three rows
	Clade 239
0.59	male palp tibia ventral apical process [320]: absent or simple swelling or part of RTA → present
	Clade 240
0.27	sternum texture [92]: smooth → rugose setal bases raised
0.43	female epigastric sclerite [203]: absent → present
0.60	dorsal scutum on male abdomen [205]: absent → present
0.44	male epigastric sclerite [207]: absent → present
(0.45)	piriform spigot base cuticle texture [261]: longitudinal ridges → smooth
(0.40)	lumen of secondary spermatheca [372]: secondary spermatheca blind sac with defined lumen → secondary spermatheca a pore field without its own lumen
(0.30)	copulatory duct between primary and secondary spermathecae [377]: distinct → none confluent
	Clade 241
0.42	chilum configuration [31]: paired isolated sclerites → single median sclerite
0.27	sternum texture [92]: smooth → rugose setal bases raised

just the main groups. Lehtinen's proposal was stimulating, in separating a group of two-clawed spiders with claw tufts that could then be studied in isolation from the dionychans, especially from the nightmare of clubionids, liocranids, and corinnids. His rearrangement took a new flight after the work of Homann (1971) on the tapetum of indirect eyes and his conception of lycosoids. The idea bloomed in the cladistic era, when it served as the context for the study of largely neglected groups, such as the zorocratids and the miturgid and zoropsid fauna of Australia.

Fruitful as it was, the lycosoid hypothesis is now aging and some discomfort is growing; the eutichurines and systariines, disputed between Clubionidae and Miturgidae are a flagship of this turmoil (Deeleman-Reinhold, 2001; Raven, 2009; Bonaldo et al., 2012). Eutichurines and systariines are somehow intermediate between clubionids and miturgids and they are problematic if we want to preserve the idea of a monophyletic Lycosoidea. The results presented here, with dionychans as derived "lycosoids," allow examination of the problem from a new perspective. Admittedly, this novel hypothesis is not strongly supported, but it can stand as a plausible scenario, at least with the same strength as the competing hypotheses that are available at the moment.

This analysis has a fairly dense sampling of genera of lycosoids and putative relatives, enough for decent testing of two character systems that were used to set them apart: the tapetum of indirect eyes and the locking lobes on the copulatory bulb (Homann, 1971; Griswold, 1993; Raven and Stumkat, 2005). Miturgids are usually associated to lycosoids by the grate-shaped tapetum found in some of their members, although it is known that at least *Teminius* has a canoe-shaped configuration (Silva Davila, 2003). A critical evaluation showed that this character system

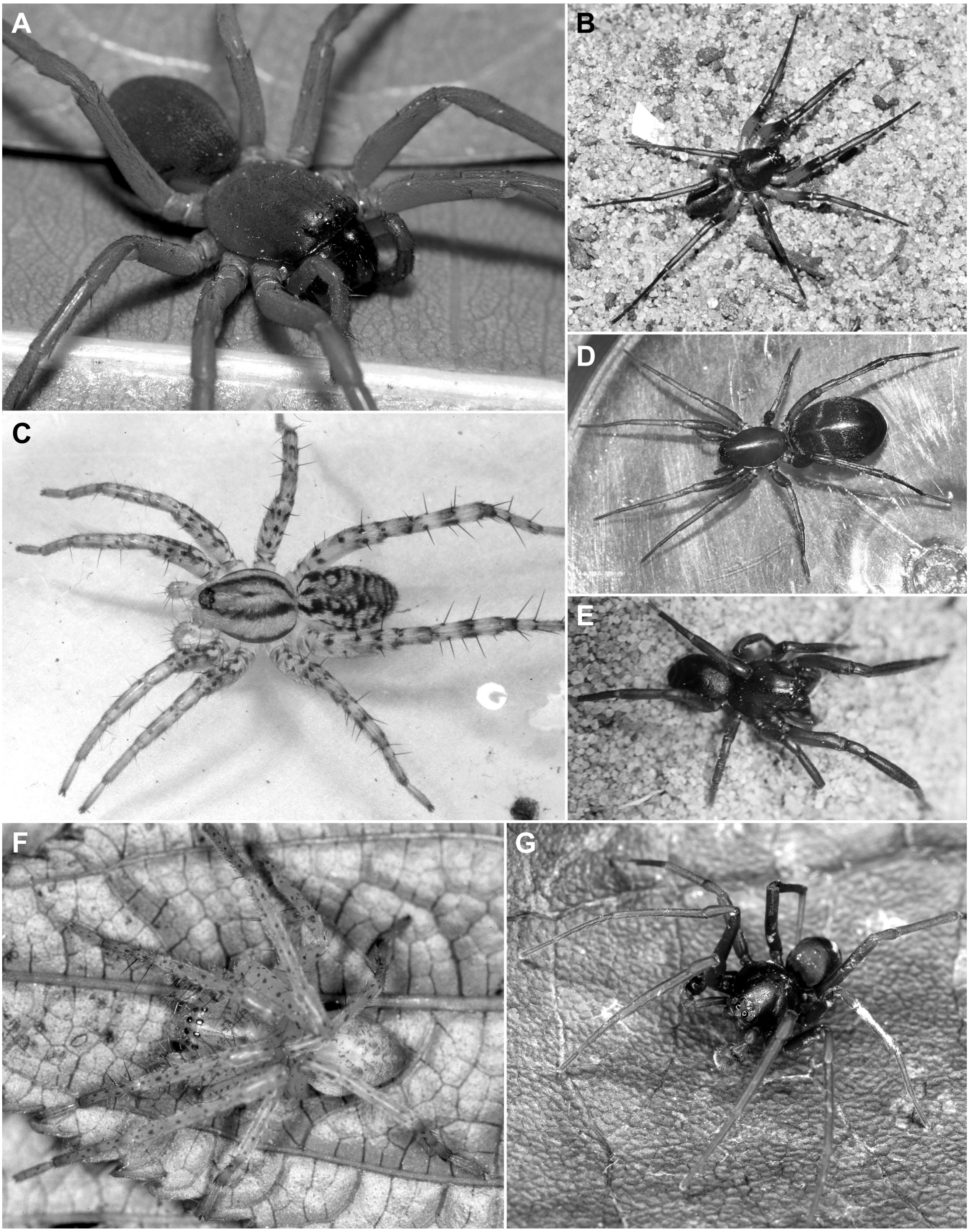


Fig. 201. Representatives of Corinnidae, habitus. **A.** *Creugas gulosus* (Corinninae; photo, Sidclay Dias). **B.** *Medmassa semiaurantiaca* (Castianeirinae; photo, Charles Haddad). **C.** *Copa* sp. (Castianeirinae; photo, Rudy Jocqué). **D.** *Castianeira longipalpa* (Castianeirinae: photo, Tom Murray). **E.** *Pronophaea natalica* (*Pronophaea* group; photo, Charles Haddad). **F.** *Olbus jaguar* (*Pronophaea* group). **G.** *Pseudocorinna* sp. (*Pronophaea* group; photo, Jan Bosselaers).

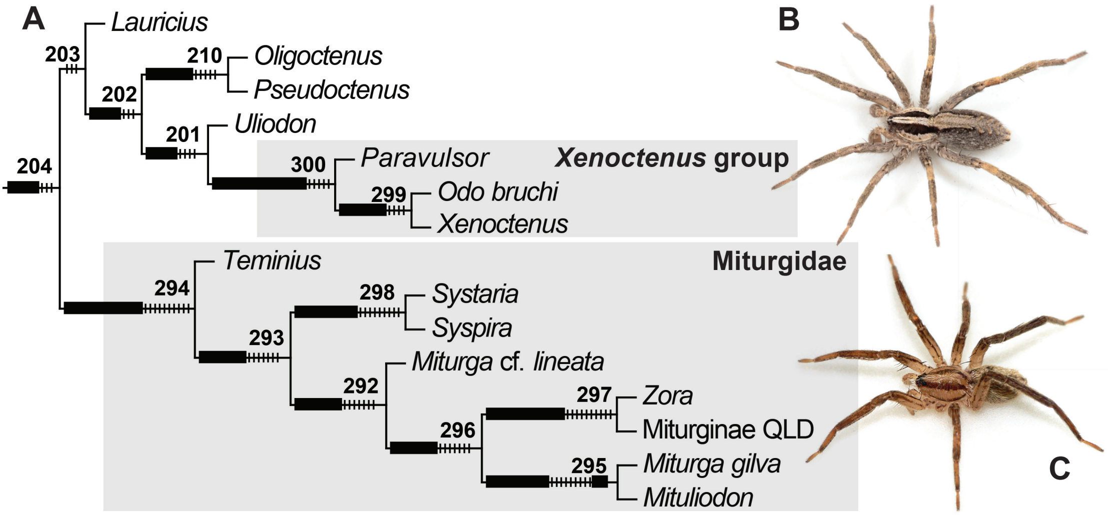


Fig. 202. **A.** Cladogram of Miturgidae, the *Xenoctenus* group, and related clades. **B.** *Odo bruchi* (*Xenoctenus* group). **C.** *Zora spinimana* (Miturgidae; photo, Aloysius Staudt).

is much more homoplasious than previously thought (fig. 194A, B; see also Silva Davila, 2003; Gray and Smith 2008). Perhaps more disturbing is the finding of a primitivelike tapetum in all indirect eyes of most Eutichuridae (as well as in *Systaria* and *Liocranoides*). The tegular and subtegular locking lobes show extensive homoplasy as well (fig. 194C, D). After the examination of many terminals with articulate embolus, it becomes clear that the tegular lobe is homologous to the embolar base (as in Griswold et al., 2005: char. 116), and that tegular or subtegular lobes may occur independently of the occurrence of an opposing lobe to lock with. Another remarkable finding is the occurrence in Miturgidae QLD of a complex sexual dimorphism in the ALS previously known only for clubionids and some "liocranids" (fig. 222).

MITURGIDAE

It seems now clear that the Zoridae are closely related to the Miturginae, and even Simon already had trouble distinguishing *Zora* from Australian miturgids (1897: 106, footnote). In an analysis of lycosoids, Silva Davila (2003) included several representative genera of Zoridae and Miturgidae, strictly defined as close to *Zora* and *Miturga* cf. *lineata*, respectively (fig. 202, table 15). Both clades were united by having a retrolateral cymbial groove (char. 331) and the embolus conformation, among other characters. Raven and Stumkat (2005) obtained similar groupings. The present analysis diverges in the interpretation and inclusion of characters from both studies, but still obtained similar results, this time with *Zora* nested within Miturginae. The male genitalia of zorids and miturgines are strikingly similar (figs. 145, 146); they have a median apophysis continuing the profile of the embolus base (char. 358), the canal on the RTA (char. 316, reversed in *Zora* but present in other zorids, e.g., *Tuxoctenus*, Raven, 2008: fig. 2), an accessory sclerite that may be present near the base of the median apophysis (char. 362 state 3; Raven, 2008: fig. 2), and a groove on the retrolateral side of the cymbium (char. 331). According to Raven and Stumkat (2003) miturgids can be distinguished from zorids by having a membranous area on the RTA. Silva Davila (2003: 45) proposed a further synapomorphy for zorids, a basal expansion of the RTA resembling a transparent wing. It was not possible to score the flat expansion of the RTA in this dataset (many intermediate conditions existed), but a species of the zorid genus *Elassoctenus* has a bulging, rather than flat basal expansion of the RTA, with a membranous area similar to

TABLE 15

Synapomorphies of Miturgidae and internal clades

See figure 202A for clades, and table 11 for conventions.

RI	**Miturgidae, Clade 294**
0.42	major ampullates, number in male [258]: one plus nubbin → two
0.30	RTA sclerotization [315]: all sclerotized → with membranous area
0.53	RTA with canal [316]: canal absent → canal present
0.64	retrolateral cymbial groove [331]: absent → present
1.00	median apophysis continuous with embolus, base directed forward [358]: other conformations → present
	Clade 292
0.61	ALE tapetum type [22]: canoe → grate
0.63	PME tapetum type [25]: canoe → grate
	Clade 293
0.55	piriform spigots size sexual dimorphism [266]: about same size in male and female → male piriforms larger
	Clade 295
0.37	metatarsal trichobothria rows [188]: single row → two or three rows
0.36	male PMS minor ampullates, number [274]: one plus nubbin → two
0.50	cymbial groove setae thickness [332]: thin or absent → thick setae
	Clade 296
0.67	female palpal tarsus apical tenent tuft [79]: absent → of pseudotenent setae
0.53	PMS cylindrical gland spigots, number [283]: many → 4, or 3
0.59	PLS cylindrical gland spigots, number [295]: 6 or more → 4, or 3
	Clade 297
0.49	posterior eye row curvature [10]: approximately straight → notably recurved
0.50	serrula width [76]: wide bordering apex → very short
0.22	detached intercoxal sternum extensions [96]: present → absent
0.44	subtegular locking lobe [341]: present → absent
	Clade 298
0.50	aciniform spigot shaft barbs [279]: only shallow sculpture or smooth → well defined barbs
0.29	secondary spermatheca size, relative to primary spermatheca [373]: smaller than primary spermatheca → larger than primary spermatheca

that found in miturgids (fig. 145D). A constrained analysis with *Zora* excluded from Miturgidae resulted in these placed as sister groups (FD = 5.76, C/F = 1.27; table S10, see supplementary data: http://dx.doi.org/10.5531/sd.sp.4). Only experiment 8, which considered most characters as unordered (table 3), produced a resolution with *Zora* sister to all other miturgids.

This analysis recovered *Systaria* nested within Miturgidae; this genus fits poorly within miturgids because, among other things, it lacks a median apophysis, but it shares with the more classical members the membranous area and canal on the RTA, and the cymbial groove (chars. 315, 316, 331; see also Platnick and Bonaldo, 1995). Excluding *Systaria* from the calculation of Bremer supports (but not from the analysis) produces a significant increase in the support of the basal branch of Miturgidae (from 8.98 to 15.02), confirming that the genus introduces conflict in the characters of the family. As noted above, *Systaria* has been at the center of the discussion of the limits of Clubionidae, Eutichurinae, and Miturgidae. Several alternative placements of *Systaria* are discussed below (figs. 204C–E, tables S5–S7).

This study also reproduces Silva Davila's (2003) finding of a clade formerly ascribed to Zoridae, which might deserve separate family status. She identified the *Xenoctenus* group, here recovered again by a peculiar division of the tegulum (char. 343), and represented by *Xenoctenus*, *Odo*, and *Paravulsor* (fig. 202, table 16). A constrained analysis indicates that it is unlikely that *Zora* may belong with the *Xenoctenus* group (FD = 12.15, C/F = 1.37; table S11, see supplementary data: http://dx.doi.org/10.5531/sd.sp.4). For the

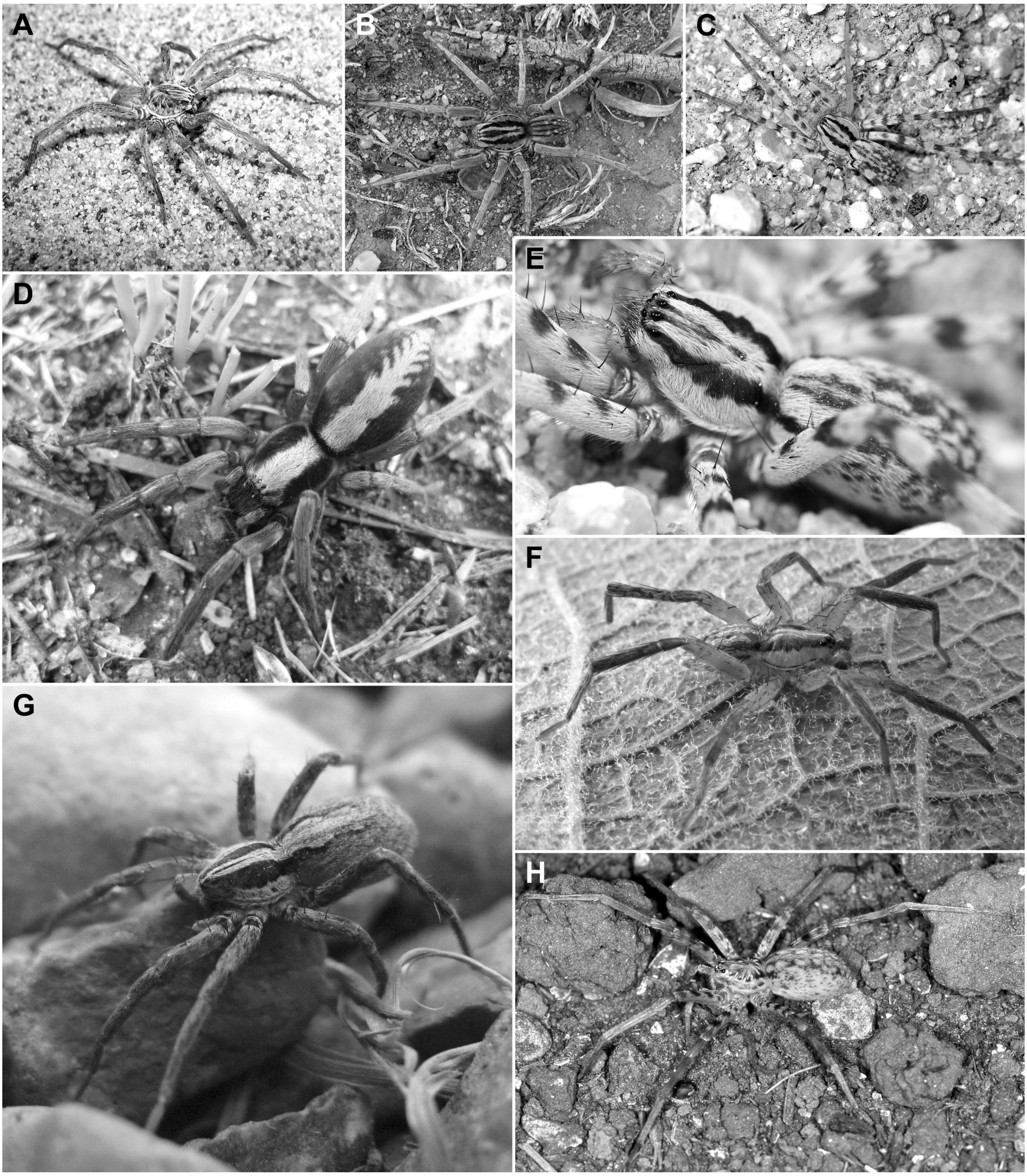


Fig. 203. Representatives of Miturgidae and the *Xenoctenus* group, habitus. **A.** *Mituliodon tarantulinus* (photo, Robert Raven). **B.** *Miturga lineata* (photo, Robert Raven). **C.** *Syspira* sp. immature (photo, Marshal Hedin). **D.** Same, close-up. **E.** *Teminius agalenoides* female (photo, Cristian Grismado). **F.** *Zora spinimana* male (photo, Jan Bosselaers). **G.** *Odo bruchi* female (photo, Cristian Grismado). **H.** *Xenoctenus* sp. immature.

TABLE 16
Synapomorphies of groups near Miturgidae and *Xenoctenus* group
See figure 202A for clades, and table 11 for conventions.

RI	**Clade 201**
0.25	embolus prolateral furrow [353]: absent → present
	Clade 202
0.31	tarsal organ opening shape [127]: round to oval → teardrop or keyhole
0.37	metatarsal trichobothria rows [188]: single row → two or three rows
0.30	copulatory duct between primary and secondary spermathecae [377]: distinct → none confluent
	(Clade 203)
(0.44)	tegular (embolar base) locking lobe [342]: absent → present
(0.29)	secondary spermatheca size, relative to primary spermatheca [373]: smaller than primary spermatheca → about as large as primary spermatheca
	Clade 204
0.71	claw tuft insertion [173]: delimited plate separated by soft area from lateral cuticle → continuous with lateral cuticle
0.44	subtegular locking lobe [341]: absent → present
	Clade 210
0.50	serrula width [76]: wide bordering apex → very short
(0.71)	claw tuft insertion [173]: continuous with lateral cuticle → delimited plate separated by soft area from lateral cuticle
0.49	embolus attachment [351]: flexibly attached → fixed
	***Xenoctenus* group, Clade 300**
0.50	female PMS minor ampullates, number [273]: two → one no nubbin
1.00	tegular distal division at embolar base [343]: absent → present projecting forward membranous limits
0.26	cuticular glands on epigyne [376]: absent → present
	Clade 299
0.49	posterior eye row curvature [10]: approximately straight → notably recurved
1.00	female palpal tarsus scopula of tenent setae [78]: absent → scopula lateral and dorsal
0.71	claw tuft [163]: of pseudotenent setae with acute tip, or of tenent setae with widened tip → absent
0.21	epigynum teeth on LL [366]: absent → present

time being, the *Xenoctenus* group can stay placed among the miturgids, as they were before among zorids.

EUTICHURIDAE

The clade 290 (figs. 204, 205; table 17), roughly corresponds to the subfamily Eutichurinae as delimited by Bonaldo (1994). The group has been recently placed either in Miturgidae (Platnick and Shadab, 1989; Bonaldo and Brescovit, 1992; Ramírez et al., 1997) or Clubionidae (Deeleman-Reinhold, 2001; Raven and Stumkat, 2003, 2005; Silva Davila, 2003; Raven, 2009), with the latter option being favored in recent phylogenetic analyses. Several of the characters used in support of either alternative are critically revised here (e.g., tapetum type, cylindrical gland spigots), suggesting that the eutichurines may better belong to its own family, not clearly related to either Clubionidae or Miturgidae. A constrained analysis forcing *Eutichurus* and *Miturga* cf. *lineata* to make up a monophyletic group, allowing (but not forcing) the inclusion of all potential miturgids, eutichurids, or anyphaenids, produced a tree only slightly suboptimal, but with a grouping of Eutichuridae + Miturgidae not supported by any synapomorphy (i.e., merely grouped by the constraint). An equivalent analysis with *Eutichurus* and *Clubiona* also produced a slightly suboptimal tree with Eutichuridae sister to Clubionidae, supported by having the chilum entire instead of paired, precoxal triangles, and lacking a subtegular locking lobe (chars. 31, 95, 341). None of those configurations seems especially attractive.

The reported absence of cylindrical gland spigots in Eutichuridae suggested a close association with other dionychans such as Anyphaenidae, and especially Clubionidae

TABLE 17

Synapomorphies of Eutichuridae and internal clades

See figure 202A for clades, and table 11 for conventions.

RI	**Eutichuridae, Clade 290**
0.61	ALE tapetum type [22]: canoe → primitive (many holes)
0.63	PME tapetum type [25]: canoe → primitive
0.35	abdomen anterior dorsal strong curved setae [213]: present → absent
	Clade 287
1.00	cymbial groove posterior extension [333]: not extended → extended as conductor
	Clade 288
0.54	epiandrous spigots [214]: present → absent
0.64	retrolateral cymbial groove [331]: absent → present
0.35	cymbial retrobasal process [335]: absent → present
0.33	mating plug–epigyne interaction [368]: mating plug small or absent → median cavity filled by mating plug
	Clade 289
0.60	promarginal escort seta [52]: present → absent
0.17	palpal claw teeth [86]: one to several teeth → no teeth
0.30	cymbial apical ventral setae [326]: sparse regular → bunch thick
	Clade 291
0.37	metatarsal trichobothria rows [188]: single row → two or three rows
0.36	male PMS minor ampullates, number [274]: one plus nubbin → two
0.50	aciniform spigot shaft barbs [279]: only shallow sculpture or smooth → well defined barbs
(0.15)	embolar basal process [352]: absent → present

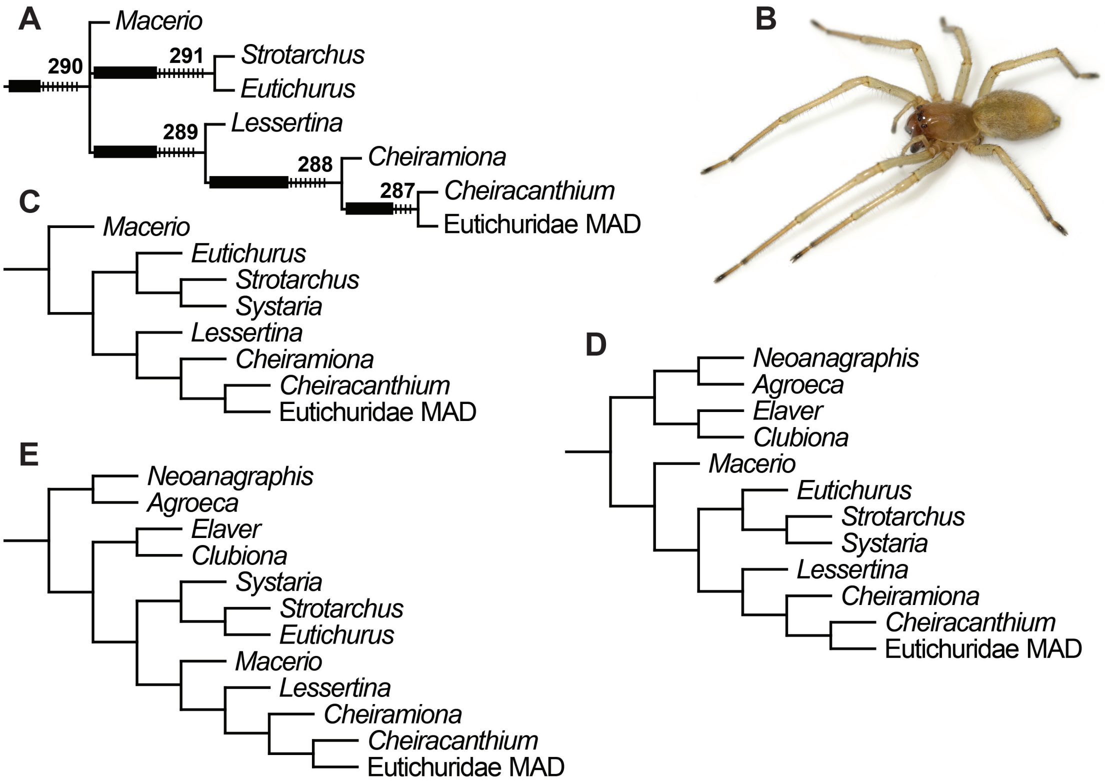

A
Macerio
290
291
Strotarchus
Eutichurus
289
Lessertina
288
Cheiramiona
287
Cheiracanthium
Eutichuridae MAD
B
C
Macerio
Eutichurus
Strotarchus
Systaria
Lessertina
Cheiramiona
Cheiracanthium
Eutichuridae MAD
D
Neoanagraphis
Agroeca
Elaver
Clubiona
Macerio
Eutichurus
Strotarchus
Systaria
Lessertina
Cheiramiona
Cheiracanthium
Eutichuridae MAD
E
Neoanagraphis
Agroeca
Elaver
Clubiona
Systaria
Strotarchus
Eutichurus
Macerio
Lessertina
Cheiramiona
Cheiracanthium
Eutichuridae MAD

Fig. 204. **A.** Cladogram of Eutichuridae. **B.** *Cheiracanthium punctorium* (photo, Arno Grabolle). **C–E.** Alternative resolutions of Eutichuridae, Clubionidae, and Systariinae using constrained searches (see tables S5, S6, S8, S9).

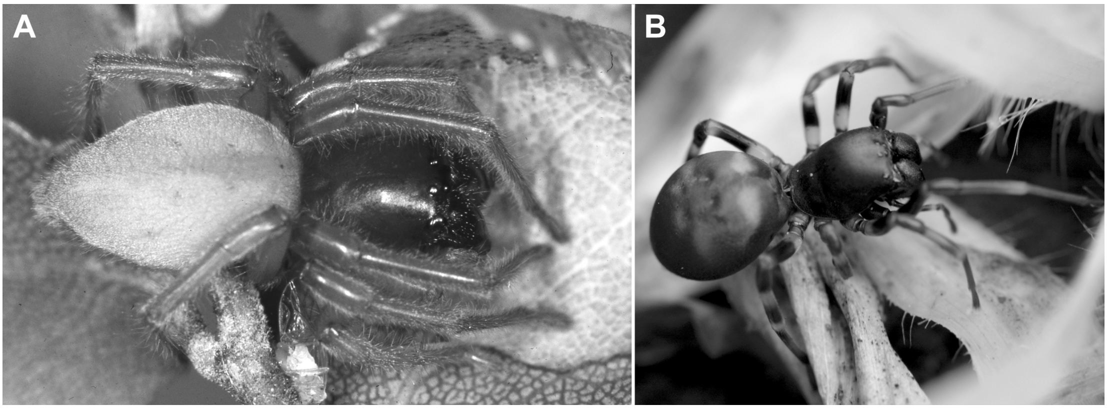


Fig. 205. Representatives of Eutichuridae, habitus. **A.** *Macerio nicoleti* female. **B.** *Lessertina mutica* female (photo, Charles Haddad).

(Deeleman-Reinhold, 2001: 85; Silva Davila, 2003). On closer examination, it turned out that *Eutichurus* and *Macerio* have cylindrical gland spigots on both PLS and PMS. In this analysis, however, this is not the main evidence placing eutichurids apart from clubionids (here represented by *Clubiona* and *Elaver*), because a reanalysis scoring those spigots as absent in all eutichurids does not recover such a grouping. Clubionids are instead strongly allied to *Agroeca* and *Neoanagraphis* by several details in their sexually dimorphic ALS spinning fields.

In this analysis, *Strotarchus* is placed in Eutichuridae, even if it has a normal thoracic furrow and lacks the projecting lateral eyes. Bonaldo (1994) tentatively transferred the genus to Miturginae, but this dataset does not support such alternative: a constrained analysis resulted in *Strotarchus* as sister to all other miturgids, not supported by any synapomorphy. When *Strotarchus* and *Systaria* are forced as sister groups (FD = 6.58, C/F = 1.30; fig. 204C; table S5, see supplementary material: http://dx.doi.org/10.5531/sd.sp.4), the grouping is mainly opposed by the RTA canal and the cymbial groove, but favored by the tapetum conformation.

The placement of cf. Eutichuridae QLD far from Eutichuridae is unconvincing (fig. 207); its male palp is very similar to that of eutichurids, especially to Eutichuridae MAD

TABLE 18

Character fit variation for an alternative resolution of Eutichuridae

Individual contribution of variations in fit from each character for the alternative resolution of figure 206D (FD = 4.44, C/F = 1.14). See figure 206 for conventions and Phylogenetic Analysis Methodology.

(c) cymbial groove posterior extension [333] = 10.00
(c) median tracheae branching [225] = 5.26
(c) median tracheae passing to carapace [226] = 4.29
(c) retrocoxal hymen size [103] = 3.31
(c) lateral tracheae branching [220] = 2.94
(c) position of openings posterior respiratory system [221] = 2.14
…
(f) cymbial tip apical thick setae [327] = −1.39
(f) PME tapetum type [25] = −1.95
(f) cymbial retrobasal process [335] = −1.95
(f) cymbial apical ventral setae [326] = −3.75
(f) ALE tapetum type [22] = −4.09
(f) epigastric median tracheae [218] = −10.00

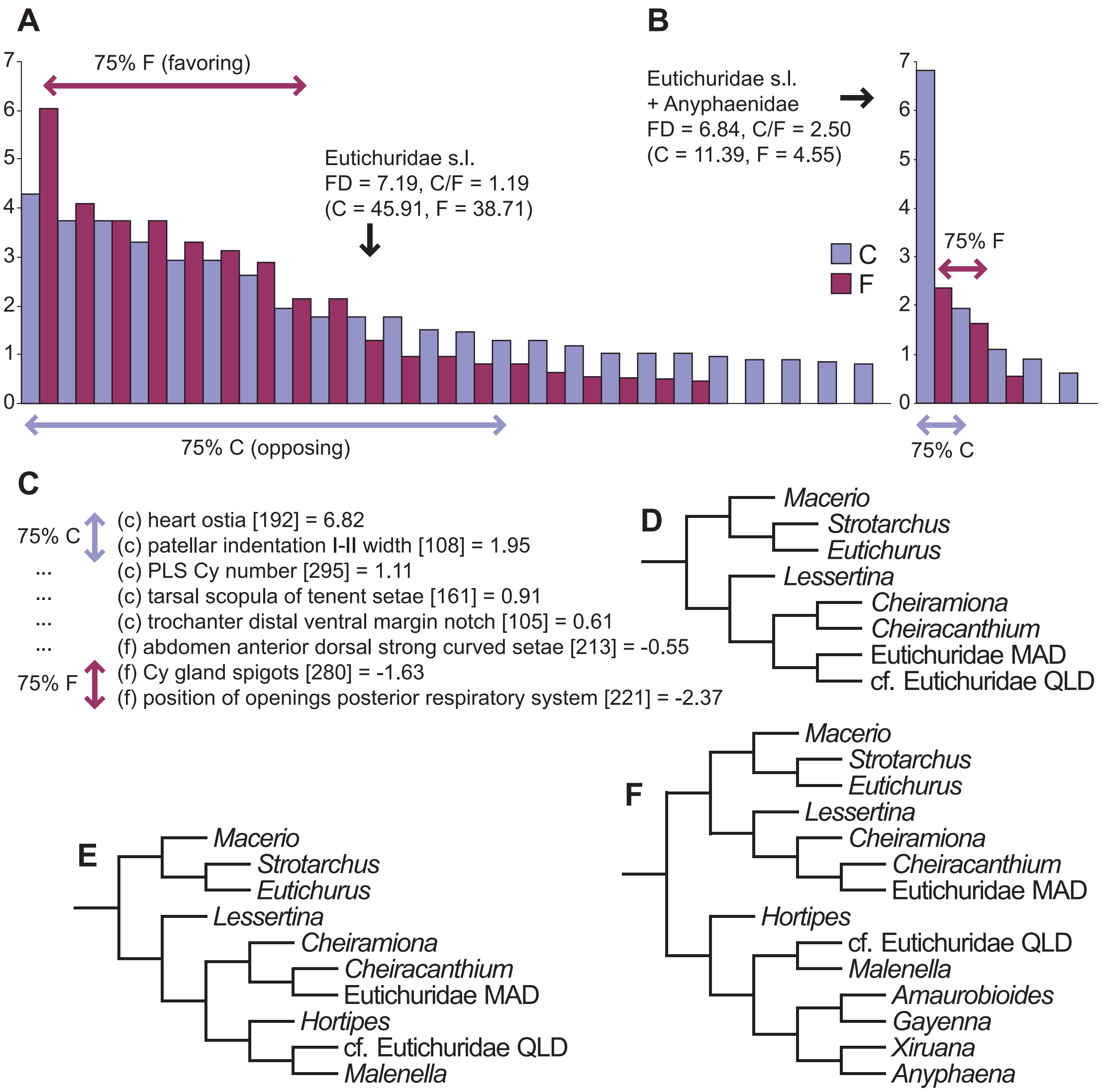


Fig. 206. **A–C.** Analysis of character performance under alternative resolutions using constrained searches, as seen in the fit profiles for characters opposing (c) and favoring (f) an alternative resolution. **A.** Example with low C/F, indicating a relatively high secondary signal (resolution shown in E; see table S3). **B.** Example with large C/F, indicating that relatively few characters are favoring such an alternative group (resolution shown in F). **C.** Individual contribution of variations in fit from each character, from the example in B and F. **D–F.** Alternative resolutions of Eutichuridae adding potential members with complex tracheae and from Anyphaenidae (see table 18).

(figs. 148E, 149B). Because of their highly developed tracheal system, cf. Eutichuridae QLD and *Hortipes* group together with anyphaenids, but this should be reevaluated after a denser sampling of eutichurids (an undescribed *Calamoneta* from Australia still has four simple tracheae as in *Eutichurus*). The experiments with the ordering of multistate characters show that any of experiments 5 through 9 (table 3) resulted in cf. Eutichuridae QLD as sister to Eutichuridae MAD, and all the eutichurids as in figure 206D. In

TABLE 19

Synapomorphies of Anyphaenidae and related groups with complex tracheae

See figure 205A for clades, and table 11 for conventions.

RI	**Clade 260**
0.48	ALE-PLE tubercle [6]: absent, slightly elevated or only ALE protruding → present, on common tubercle
0.68	patellar indentation I–II width [108]: narrow → wide
(0.67)	tarsal scopula of tenent setae [161]: present → absent
(0.35)	abdomen anterior dorsal strong curved setae [213]: present → absent
	Clade 261
(0.31)	tarsal organ opening shape [127]: round to oval → teardrop or keyhole
0.62	lateral tracheae branching [220]: simple, linear → branched
0.59	median tracheae branching [225]: unbranched → strongly branched
0.62	median tracheae passing to carapace [226]: limited to abdomen → two large trunks with many ramifications passing to carapace
	Clade 286
0.45	thoracic fovea [0]: present → absent
0.53	female palpal tarsus dorsal chemosensory setae distribution [83]: scattered → in a defined patch
(0.55)	scales [157]: present → absent
0.40	lumen of secondary spermatheca [372]: secondary spermatheca blind sac with defined lumen → secondary spermatheca a pore field without its own lumen
0.26	receptacle in copulatory duct, in addition to primary and secondary spermathecae [374]: absent → between copulatory opening and primary spermatheca
	Anyphaenidae, Clade 284
0.38	claw tuft setae tenent surface orientation [172]: facing ventrally → facing mesally
0.71	claw tuft insertion [173]: delimited plate separated by soft area from lateral cuticle → continuous with lateral cuticle
0.44	cymbial tip ventral groove [323]: absent → present
	Anyphaeninae, Clade 283
0.48	trochanter distal ventral margin notch [105]: shallow or absent → deep at least legs I–II
0.50	position of openings posterior respiratory system [221]: slightly separated from spinnerets → well advanced closer to epigastrium
	Amaurobioidinae, Clade 285
(0.55)	scales [157]: present → absent
0.55	cymbium dorsal chemosensory patch [324]: present → absent
0.44	subtegular locking lobe [341]: absent → present
0.44	tegular (embolar base) locking lobe [342]: absent → present
1.00	tegular notches [344]: none → Amaurobioidinae-like
0.15	embolar basal process [352]: absent → present
0.18	other tegular articulate sclerites [362]: none → at base of conductor

fact, only making the characters 283 and 293 (counts of cylindrical gland spigots on PMS and PLS) unordered suffices to produce such a resolution (C/F = 1.14, table 18). Including cf. Eutichuridae QLD, *Hortipes*, and *Malenella* in Eutichuridae is also a promising alternative (C/F = 1.19; fig. 206E; table S3, see supplementary material: http://dx.doi.org/10.5531/sd.sp.4). It seems clear, however, that *Malenella* is not well placed as the most basal Anyphaenidae, excluding *Hortipes* and cf. Eutichuridae QLD (C/F = 2.32, table S4 in supplementary data).

Anyphaenidae and Other Groups with Complex Tracheae

A charismatic character system usually associated with Anyphaenidae is their complex tracheal system (Forster, 1970; Platnick, 1974; Ramírez, 1995, 2003). As illustrated by Lamy (1902), several distantly related spiders have a perplexingly similar tracheal system (e.g., some Uloboridae and Prodidomidae), and an additional instance is reported here for the enigmatic genus *Hortipes*, formerly placed in Liocranidae and Corinnidae (Bosselaers and Jocqué 2000, 2002), and joined

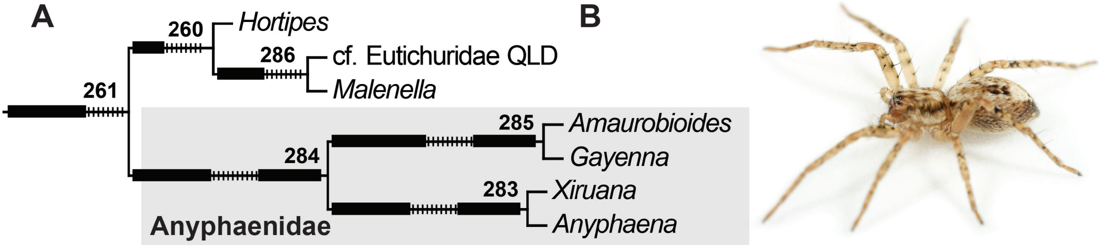

A
260
Hortipes
286
cf. Eutichuridae QLD
Malenella
261
285
Amaurobioides
Gayenna
284
283
Xiruana
Anyphaena
Anyphaenidae
B

Fig. 207. **A.** Cladogram of Anyphaenidae and related groups with complex tracheae. **B.** *Anyphaena accentuata* (photo, Stefan Sollfors).

here together with anyphaenids and a euticHuridlike terminal with complex tracheae (fig. 207, table 19). These convergences in the details of complex tracheal systems suggest that they may obey a common signaling during development, probably used for more general purposes. The tracheal configurations are both homoplasious and informative. The branching of tracheae usually affects both the laterals and the medians

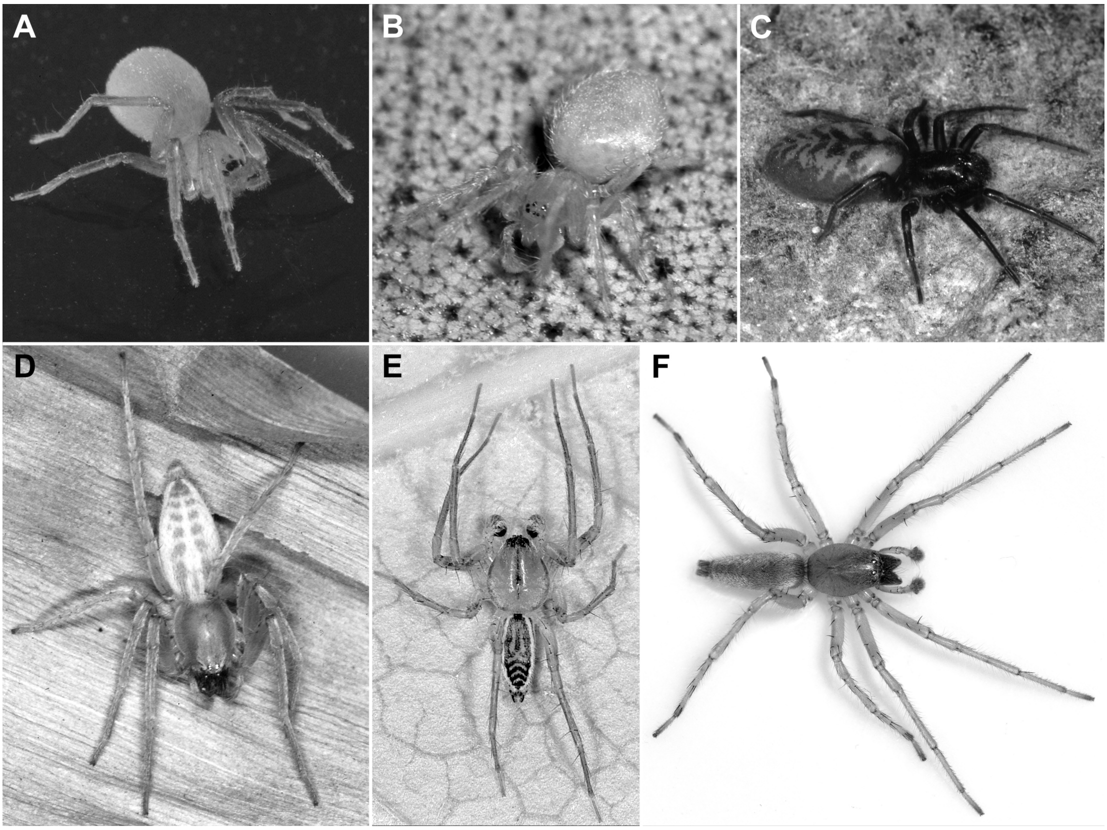


Fig. 208. Representatives of Anyphaenidae, probably related groups with complex tracheae, and Clubionidae. **A.** *Hortipes merwei* female (photo, Hans Henderickx). **B.** *Malenella nana* female. **C.** *Amaurobioides chilensis* female. **D.** *Xiruana hirsuta* female. **E.** *Gayenna americana* female. **F.** *Clubiona pallidula* male (photo, Arno Grabolle).

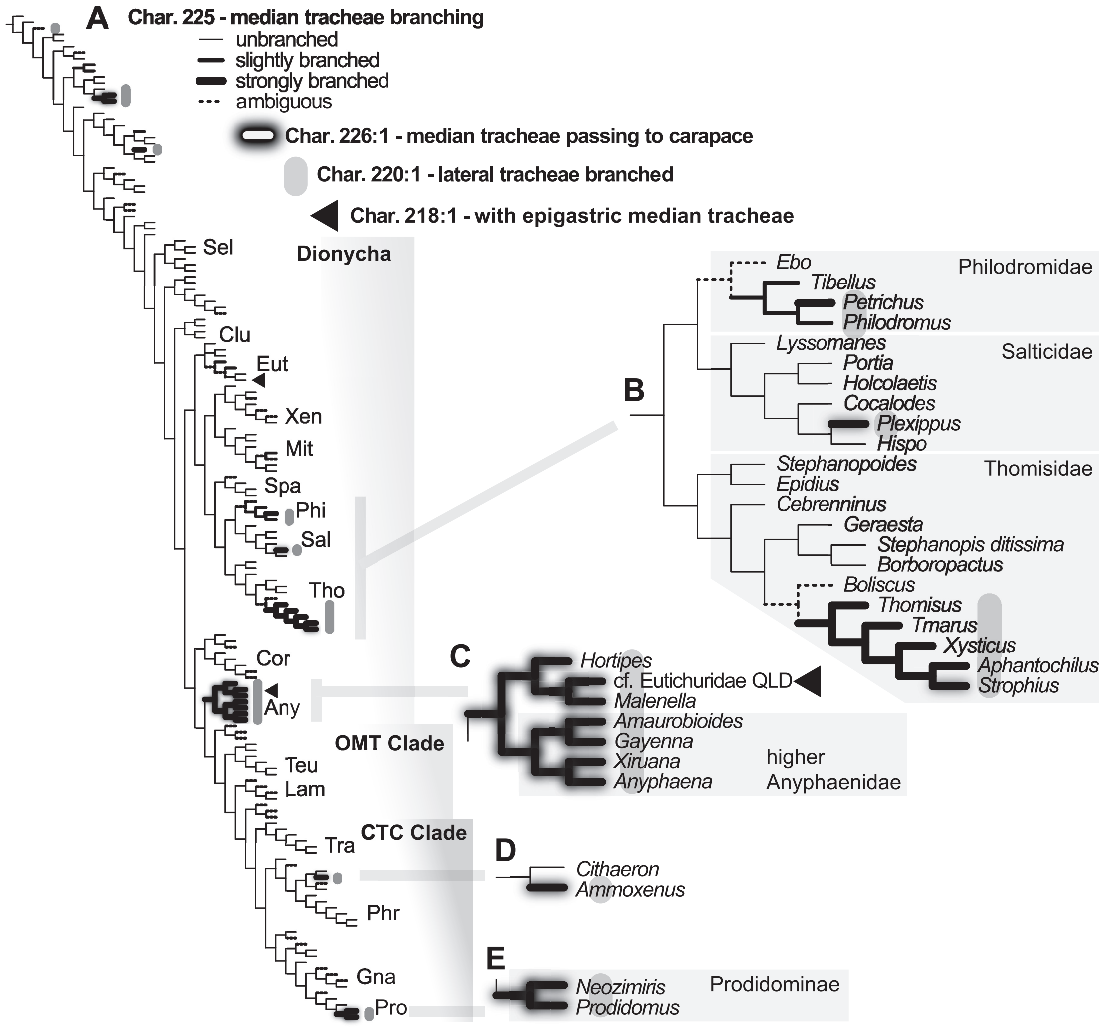

A
Char. 225 - median tracheae branching
unbranched
slightly branched
strongly branched
ambiguous
Char. 226:1 - median tracheae passing to carapace
Char. 220:1 - lateral tracheae branched
Char. 218:1 - with epigastric median tracheae
Sel
Dionycha
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Cor
Any
OMT Clade
Teu
Lam
Tra
CTC Clade
Phr
Gna
Pro
B
Ebo
Tibellus
Petrichus
Philodromus
Philodromidae
Lyssomanes
Portia
Holcolaetis
Cocalodes
Plexippus
Hispo
Salticidae
Stephanopoides
Epidius
Cebrenninus
Thomisidae
Geraesta
Stephanopis ditissima
Borboropactus
Boliscus
Thomisus
Tmarus
Xysticus
Aphantochilus
Strophius
C
Hortipes
cf. Eutichuridae QLD
Malenella
Amaurobioides
Gayenna
Xiruana
Anyphaena
higher Anyphaenidae
D
Cithaeron
Ammoxenus
E
Neozimiris
Prodidomus
Prodidominae

Fig. 209. Mapping of tracheal characters. The branching of the median and lateral tracheae usually occurs coordinately, and the extension of the median tracheae into the carapace occurs in taxa with extensively branched tracheae. The two terminals with epigastric median tracheae (Eutichuridae MAD and cf. Eutichuridae QLD) might be closely related (see alternative resolution in fig. 206D). **A.** Bird's eye view of the characters on the entire tree. **B.** Detail of Salticidae and crab spiders. **C.** Detail of anyphaenids and related groups with complex tracheae. **D, E.** Detail of groups of the OMT clade with complex tracheae.

coordinately, and the passing of the medians to the carapace occurs together with, and often preceded by, a highly branched tracheal system (fig. 209). Two species of eutichurid-like undescribed genera (Eutichuridae MAD and cf. Eutichuridae QLD) are here reported to have a novel type of tubular tracheae between the anterior book lungs, the epigastric median tracheae (char. 218).

The higher anyphaenids (Anyphaeninae and Amaurobioidinae) are well supported in this analysis, but the placement of *Malenella* should be reevaluated after more eutichurid-like representatives are included. Amaurobioidinae is supported, among other characters, by the tegular notch (char. 344) and the paramedian apophysis (char. 362) (Ramírez, 2003, 2007).

TABLE 20

Synapomorphies of Clubionidae and related groups

See figure 208A for clades, and table 11 for conventions.

RI	**Clubionidae, Clade 215**
0.22	detached intercoxal sternum extensions [96]: absent → present
0.54	epiandrous spigots [214]: present → absent
0.52	cylindrical gland spigots [280]: present → absent
	Clade 216
0.68	demarcation between major ampullate and piriform fields [264]: major ampullate field integrated with piriform field or no furrow → separated by deep furrow only male
0.75	male separate major ampullate field with smaller piriforms [265]: separate field only major ampullates → some small piriforms with the major ampullates
0.55	piriform spigots size sexual dimorphism [266]: about same size in male and female → male piriforms larger
0.91	ALS basal article cylindrical, with inflatable piriform field [268]: absent, ALS truncate cone → present in males
	***Neoanagraphis* + *Agroeca*, Clade 242**
0.23	male tarsus IV curvature and cuticle [125]: straight or continuos cuticle → bent, pseudosegmented
0.48	scales setules [159]: absent → present
0.71	claw tuft [163]: of tenent setae with widened tip → absent
0.75	embolus tip wide truncate opening on thin transverse tube [355]: absent → present

Clubionidae and Allies

The strictly defined Clubionidae (the Clubioninae in, e.g., Deeleman-Reinhold, 2001), here represented by *Clubiona* and *Elaver* (fig. 208F; clade 215 in fig. 210; table 20), obtained moderate support from reversions of a few homoplasious characters, such as the loss of the cylindrical gland spigots (see Platnick, 1990: 41). Besides the few synapomorphies and low Bremer support, the group is not much disputed, as evidenced by its high jackknifing frequency and stability to weighting regimes. Clubionids and two genera usually placed in Liocranidae, *Agroeca* and *Neoanagraphis*, are here united by a characteristic sexual dimorphism in the anterior lateral spinnerets (chars. 264–266, 268; see also Platnick, 1990: 35). It is remarkable that similar sexual dimorphic configurations, involving combinations of states of this suite of characters, occur in seemingly disparate lineages, such as clubionids, some miturgids, "liocranids," and gnaphosoids (fig. 268B). *Agroeca* and *Neoanagraphis* were also found closely related by Bosselaers and Jocqué (2002); among other

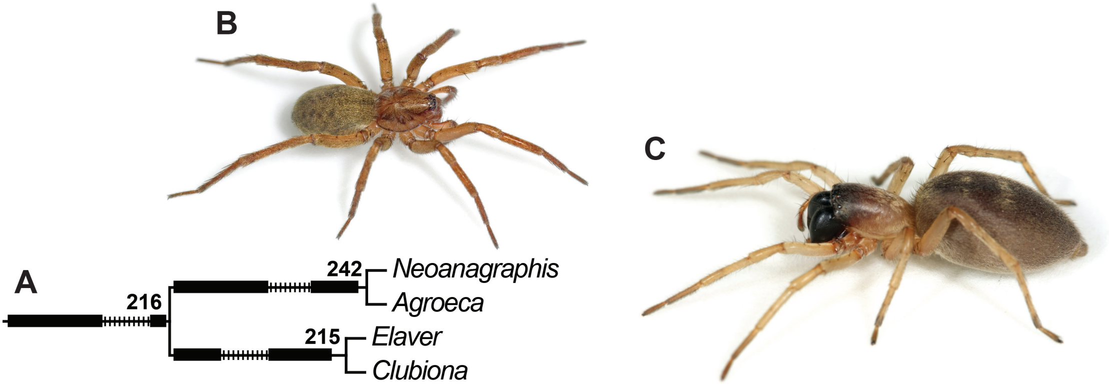


Fig. 210. **A.** Cladogram of Clubionidae and related groups with sexually dimorphic ALS. **B.** *Agroeca brunnea* female (photo, Arno Grabolle). **C.** *Clubiona phragmitis* female (photo, Stefan Sollfors).

TABLE 21

Synapomorphies of Sparassidae and internal clades

See figure 211A for clades, and table 11 for conventions.

RI	**Sparassidae, Clade 311**
1.00	metatarsal dorsodistal stopper conformation [120]: solid about straight distal border → membranous trilobate
0.50	apical ventral tarsal cuticle sclerotization [130]: entire sclerotized → unsclerotized transverse suture below claws
1.00	claw tuft seta tip profile [168]: not indented → deeply indented
1.00	membranous extensions of tarsi embracing claw tuft plate [174]: absent → present
0.90	sculpture on basal expansion of trichobothrial seta [184]: bumps → ridges or smooth
(0.71)	epiandrous spigots disposition [215]: two definite bunches → dispersed
0.49	embolus attachment [351]: flexibly attached → fixed
	Clade 312
0.60	promarginal escort seta [52]: present → absent
(0.40)	internal prolongations on book lung cover [217]: absent → present
0.64	colulus [237]: hairy plate or two setae → absent
	Clade 313
(0.18)	Labium length width ratio [68]: longer or about equal → wider than long
(0.13)	retrocoxal hymen size [103]: small to medium sized mound → large unsclerotized patch

more homoplasious characters supporting such a group, the particular conformation of the embolus tip (char. 355) is also found in clade 244 of the OMT clade (*Austrachelas*, *Liocranum*, *Apostenus*; fig. 220). The results of Bosselaers and Jocqué of *Liocranum* closely associated with clubionines can be explained by their approximate scoring of spigots from the stereomicroscope, and the difficult interpretation of spigot complement from SEM images. *Liocranum* has in fact cylindrical gland spigots (fig. 143D), and their images of *Mesiothelus* show at least one cylindrical gland spigot on PMS and PLS (their fig. 7D, F, top left in both cases).

An enhanced definition of Clubionidae to include *Systaria* and Eutichuridae is slightly suboptimal, but still shows *Agroeca* and *Neoanagraphis* as sister to Clubioninae (fig. 204D; table S8, see supplementary material: http://dx.doi.org/10.5531/sd.sp.4). Forcing the exclusion of these two genera produces far suboptimal trees without much gain in the fit of other characters (C/F = 1.81; table S9 in supplementary data), and, in addition, with both genera as sister to the remaining "Clubionidae" (fig. 204E).

SPARASSIDAE

Sparassids are clearly diagnosed by having the metatarsal dorsodistal stopper modified in a flexible, trilobate membrane (char. 120), a classical character for the family. This study reports new additional synapomorphies: a characteristically indented tip of the claw tuft setae (char. 168), the membranous extensions of the tarsi at the sides of the claw tuft plates (char. 174), and the trichobothrial setae lacking the bumps on their bases (char. 184), reversed from the condition found in the Oval Calamistrum clade, including dionychans. All those characters have either perfect or very high fit on the tree, thus Sparassidae appears well supported, except under equal weights. In this last regime Sparianthinae VEN is placed afar from the rest of Sparassidae. One further synapomorphy proposed by Rheims (2007) for the family is the presence of a dorsal chemosensory "scopula" on the male cymbium (char. 324), which is ambiguously optimized here and appears scattered across the lycosoid-dionychan lineages (CI = 0.03, RI = 0.55).

The internal structure of Sparassidae obtained in the preferred tree (see clade 313, with marginal support; table 21) is at odds with the larger phylogenetic analysis of the family by Rheims (2007), and most likely incorrect. The Sparianthinae, here represented by Sparianthinae VEN, would be expected to branch off basally, as obtained in the alternative tree of figure 211D; most alterations to the ordering of multistate characters (experiments 1, 2, 5–9, table 3) resulted in Sparianthinae sister to the rest of Sparassidae (fig. 211D, table 22). This basal position

TABLE 22

Synapomorphies of alternative resolution of Sparassidae and Selenopidae

See figure 211D for clades, and table 11 for conventions.

Sparassidae, Clade A

Same synapomorphies as Clade 311 (table 21)

Sparassidae except Sparianthinae, Clade B

ALE tapetum type [22]: canoe → hexagonal pattern of holes
PME tapetum type [25]: canoe → hexagonal pattern of holes
cymbial tip apical thick setae [327]: absent → present
median apophysis [356]: present → absent

Clade C

promarginal escort seta [52]: present → absent
colulus [237]: hairy plate or two setae → absent
secondary spermatheca size, relative to primary spermatheca [373]: smaller than primary spermatheca → about as large as primary spermatheca

Selenopidae, Clade D

PME position relative to anterior eye row [17]: posterior to AME → approximately in line with AME
trichobothria proximal plate transverse ridges [178]: with transverse ridges → smooth
cymbial apex extension beyond alveolus [325]: extending beyond distal margin of alveolus → short wide not extending

Clade E

apical ventral tarsal cuticle sclerotization [130]: entire sclerotized → unsclerotized transverse suture below claws
metatarsal trichobothria rows [188]: single row → two or three rows

seems plausible, as sparianthines are the only sparassids with median apophysis and canoe-shaped tapeta. Under this alternative resolution, all other sparassids would be united by the characteristic tapetum made of a large silvery plate with hexagonal pattern of holes (chars. 22, 25, see table 22; Homann, 1971; Land, 1985; Nørgaard et al., 2008). This tapetum reflects very intensely the light from a headlamp in night collecting (personal obs.), similar to what occurs with higher lycosoids.

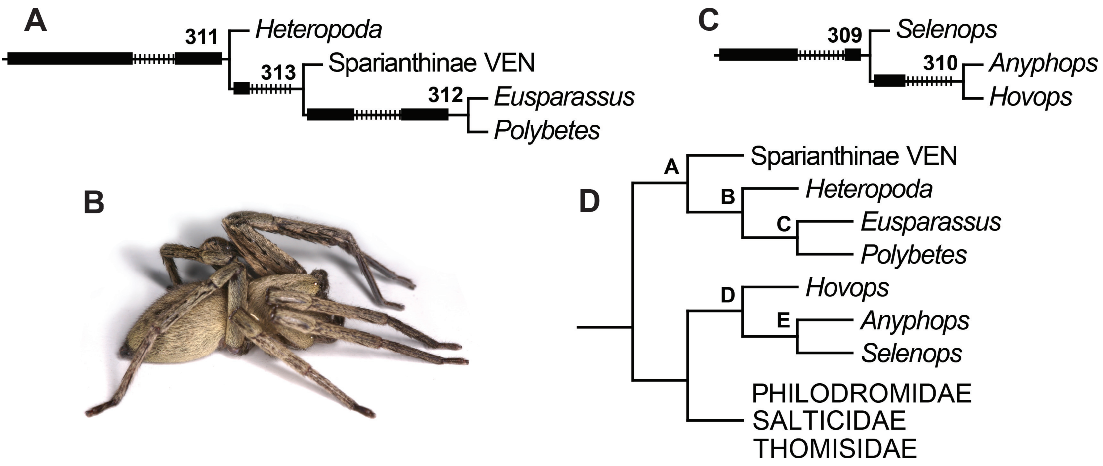

A
311
Heteropoda
313
Sparianthinae VEN
312
Eusparassus
Polybetes
C
309
Selenops
310
Anyphops
Hovops
B
D
A
Sparianthinae VEN
B
Heteropoda
C
Eusparassus
Polybetes
D
Hovops
E
Anyphops
Selenops
PHILODROMIDAE
SALTICIDAE
THOMISIDAE

Fig. 211. **A.** Cladogram of Sparassidae in the preferred tree; the position of *Heteropoda* is most likely incorrect (see text). **B.** *Thelcticopis severa* male from Laos (Sparassidae; photo, Peter Jäger). **C.** Cladogram of Selenopidae. **D.** Alternative resolution of Selenopidae and Sparassidae obtained with the scoring of the ALE tapetum of *Selenops* and *Hovops* as grate shaped.

TABLE 23

Synapomorphies of Selenopidae and internal clades

See figure 211C for clades, and table 11 for conventions.

RI	
	Selenopidae, Clade 309
1.00	PME position relative to anterior eye row [17]: posterior to AME → approximately in line with AME
0.72	leg orientation [97]: prograde → laterigrade
0.26	cymbial apex extension beyond alveolus [325]: extending beyond distal margin of alveolus → short wide not extending
0.59	conductor sclerotization [360]: hyaline or membranous → sclerotized
	Clade 310
0.48	trochanter distal ventral margin notch [105]: deep at least legs I–II → shallow or absent
0.20	cymbial retromedian process [336]: absent → present without furrow
0.49	embolus attachment [351]: flexibly attached → fixed

SELENOPIDAE

Selenopidae is mostly supported by the characteristic eye pattern of the PME advanced to the anterior eye row (char. 17). Selenopids look so characteristic that one would expect a long list of synapomorphies for the family, but I have failed to find convincing somatic or ultrastructural characters to further support the monophyly of the group (table 23, fig. 211C). This situation is even worse for the relationships of selenopids with other families, and the situation with the scoring of characters from the tapetum is useful to show the fragility of the relationships obtained here for the family. Selenopids

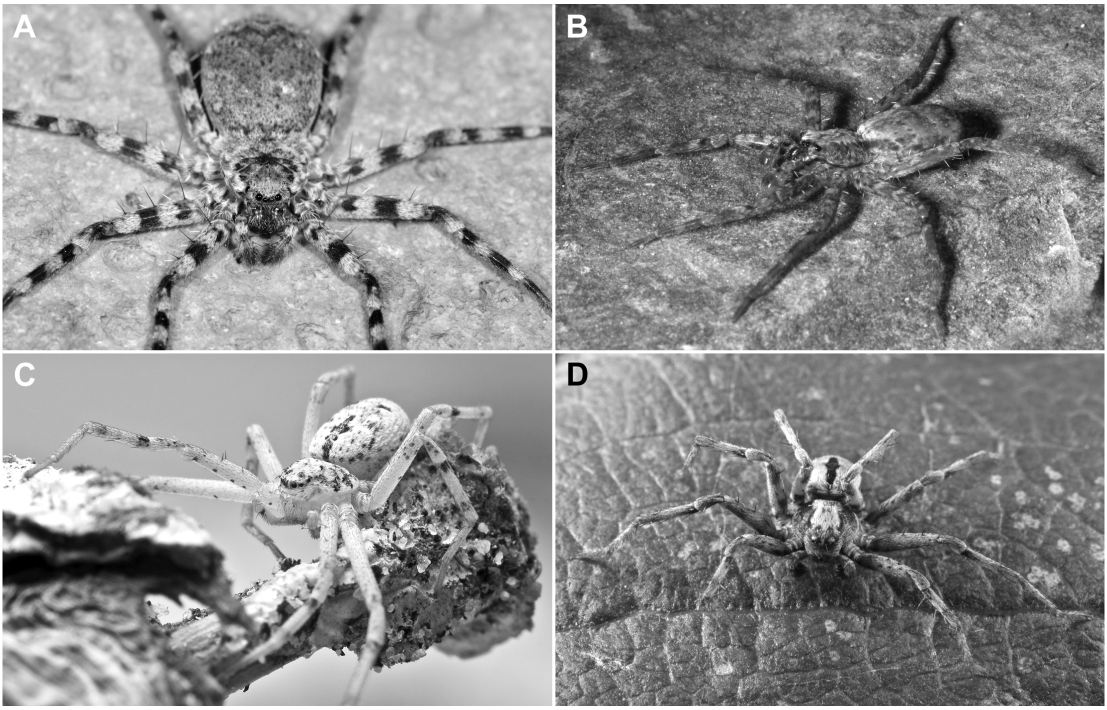


Fig. 212. Representatives of Selenopidae and Philodromidae, habitus. **A.** *Selenops* sp. immature (Selenopidae; photo, Marshal Hedin). **B.** *Anyphops stauntoni* penultimate male (Selenopidae; photo, Roger S. Key). **C.** *Ebo pepinensis* female (Philodromidae; photo, Marshal Hedin). **D.** *Petrichus* sp. (Philodromidae; photo, Jan Bosselaers).

TABLE 24

Synapomorphies of the clades uniting salticids, philodromids and thomisids

See figure 214B for clades, and table 11 for conventions.

RI	**Philodromidae + Salticidae, Clade 306**
0.73	ALE tapetum [21]: present → absent
0.56	PME tapetum [24]: present → absent
0.67	retrocoxal hymen [102]: leg I → absent
0.82	tarsal trichobothria rows [190]: two or three rows → single row
	Thomisidae + Philodromidae + Salticidae, Clade 307
0.60	promarginal escort seta [52]: present → absent
(0.48)	trochanter distal ventral margin notch [105]: deep at least legs I–II → shallow or absent
0.84	metatarsus ventroapical end extension [118]: truncate or invaginated → extending below tarsus

have greately reduced tapeta on their posterior eyes (chars. 21 to 28; fig. 194A, B), and their morphology is difficult to interpret. According to my observations and my interpretation of Homann's reports, I scored the tapetum of the posterior eyes as of uncertain type. If we follow the interpretation of Corronca (1997; see comments on chars. 24, 25) and score those as grate (char. 25, state 2), that subtle change produces a significant rearrangement in Selenopidae, Sparassidae, and their relationships with other families (fig. 211D, table 22). Preliminary versions of this dataset resulted in the enigmatic *Lauricius* (fig. 197E, F) sister to selenopids, which is only slightly suboptimal in this analysis (FD = 1.89, C/F = 1.09).

The Affiliation of Salticids and Crab Spiders

The sister group of Salticidae is a longstanding mystery of spider systematics. This analysis provides evidence for a close relationship of salticids with philodromids, and both with thomisids (fig. 214). So far, some molecular analyses of salticids or thomisids (see references in Hill and Richman, 2009) have tangentially touched on this issue by the inclusion of outgroups, but they have not obtained any consistent pattern of relationships.

Salticids and philodromids are here joined by the loss of their eye tapeta, of the retrocoxal hymen, and a reduction in tarsal trichobothria rows (table 24). Hill and Richman (2009) had suggested such a relationship, by the uncommon enlargement of the direct median eyes of philodromids, notably so in the basal genus *Ebo* (see Muster, 2009a: figs. 7–10). This grouping would remain if the loss of tapeta is considered as a single character for all eyes simultaneously, as using a weight of 0.5 for both characters 21 and 24 produces the same results. Thomisids are joined to that group notably by the extension of the metatarsus ventroapical end below the tarsus (char. 118), found only sporadically among spiders (notably in Oxyopidae and Senoculidae; see below).

Philodromidae

Most discussions on the characters relevant for Philodromidae were centered on its distinction from Thomisidae (e.g., Homann, 1975), rather than on synapomorphies for the family, which are still unclear (Muster, 2009b). The claw tuft of tenent setae in the palp of males and females is here reported as an unambiguous character state supporting the monophyly of Philodromidae (char. 79; table 25, fig. 213). Because here the character was construed as multistate, it has homoplasy in the presence of pseudotenent setae (e.g., in thomisids and miturgids), but true tenent setae on palp claw tufts are unique to philodromids. The distribution of these states suggests that the pseudotenent condition is not a precursor of true tenent setae, but a convergence (fig. 214C, see also fig. 198B). Philodromidae and its internal clades also appear strongly supported by cheliceral morphology, similar to what Homann (1975) found. The reduction of cheliceral teeth and development of cheliceral mounds are curiously paralleled in derived Thomisidae (fig. 214A, B). The results obtained here are coincident with Muster's (2009b) finding

TABLE 25

Synapomorphies of Philodromidae and internal clades

See figure 213A for clades, and table 11 for conventions.

RI	**Philodromidae, Clade 305**
0.44	cheliceral retromarginal teeth [48]: present → absent
0.67	cheliceral promarginal pronounced mound [56]: absent → present
0.65	endites obliquely depressed [70]: absent → present
0.67	female palpal tarsus apical tenent tuft [79]: absent → of tenent stae
0.48	scales setules [159]: absent → present
	Clade 304
0.67	cheliceral promarginal pronounced mound [56]: present → mound plus dark long tooth
0.53	PMS cylindrical gland spigots, number [283]: many → 3
0.59	PLS cylindrical gland spigots, number [295]: 6 or more → 4
	Clade 303
0.20	cheliceral basal posterior membranous mound [35]: absent → present
0.62	lateral tracheae branching [220]: simple, linear → branched

of a relatively basal position of the New World *Titanebo*. All other genera are united here by having a dark tooth on the promarginal cheliceral mound (char. 56, state 2).

Homann (1975) proposed a sister-group relationship between Sparassidae and Philodromidae, as suggested by the occurrence of a particular slit in the pigment cup of the indirect eyes. This character could not be scored here because of the complexity of the anatomy and the small overlap of the terminals scored here and in Homann's work. A quick test of this proposal was made scoring a pigment slit character in terminals examined by Homann (1971, 1975), as follows: *Philodromus*, *Tibellus*, *Heteropoda* = 1; *Xysticus*, *Aphantochilus* = 0; all other philodromids, sparassids and thomisids = ?; all remaining families = 0. This dataset produced a monophyletic Sparassidae + Philodromidae when the added character is weighted 1.33 relatively to the other characters. Under such a resolution, the two families would be supported by no character other than the pigment slit. Other characters mentioned by Homann (1975) are very complex and not well known (rhabdome anatomy, postembryonic development) or are already covered here (cheliceral setae, trichobothria).

THOMISIDAE

Thomisidae appears strongly supported in this analysis, even if some of the characters used in keys to distinguish the family were

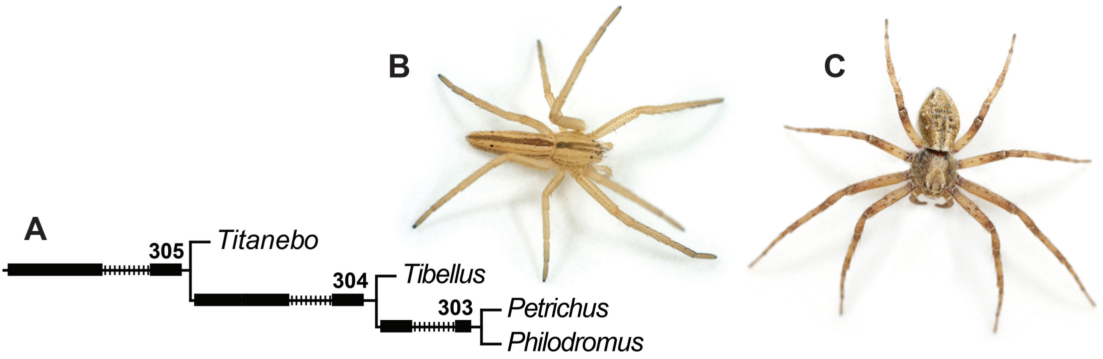


Fig. 213. **A.** Cladogram of Philodromidae. **B.** *Tibellus oblongus* female. **C.** *Philodromus aureolus* female (photos, Stefan Sollfors).

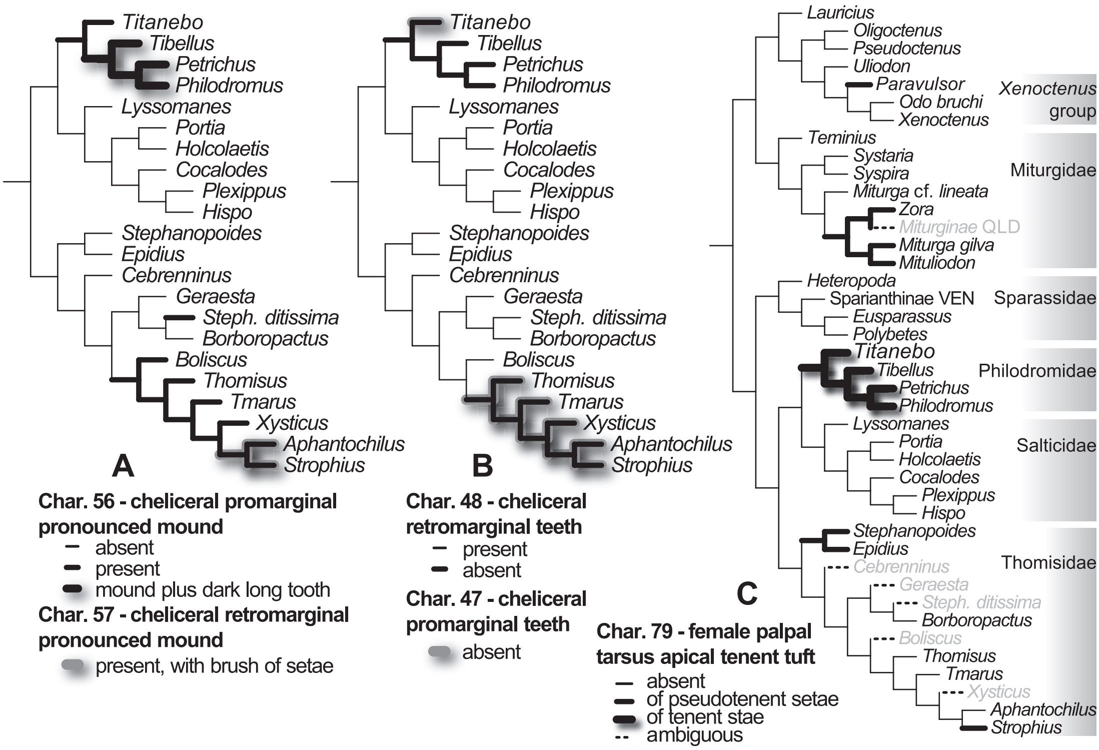

Titanebo
Tibellus
Petrichus
Philodromus
Lyssomanes
Portia
Holcolaetis
Cocalodes
Plexippus
Hispo
Stephanopoides
Epidius
Cebrenninus
Geraesta
Steph. ditissima
Borboropactus
Boliscus
Thomisus
Tmarus
Xysticus
Aphantochilus
Strophius
A
Char. 56 - cheliceral promarginal pronounced mound
absent
present
mound plus dark long tooth
Char. 57 - cheliceral retromarginal pronounced mound
present, with brush of setae
B
Char. 48 - cheliceral retromarginal teeth
present
absent
Char. 47 - cheliceral promarginal teeth
absent
Lauricius
Oligoctenus
Pseudoctenus
Uliodon
Paravulsor
Odo bruchi
Xenoctenus
Xenoctenus group
Teminius
Systaria
Syspira
Miturga cf. lineata
Zora
Miturginae QLD
Miturga gilva
Mituliodon
Miturgidae
Heteropoda
Sparianthinae VEN
Eusparassus
Polybetes
Sparassidae
Philodromidae
Salticidae
Thomisidae
C
Char. 79 - female palpal tarsus apical tenent tuft
absent
of pseudotenent setae
of tenent stae
ambiguous

Fig. 214. Mapping of characters distinctive of thomisids and philodromids. **A, B.** The cheliceral mounds and reduction of teeth have evolved convergently in Philodromidae and higher Thomisidae. **C.** The female palpal tufts of pseudo-tenent setae have appeared convergently in several groups, but tufts of true tenent setae are unique to Philodromidae.

not used here because of its quantitative basis (the longer, stouter legs I and II, and the ALE larger than the AME). Thomisids are here joined by a suite of homoplasious characters, such as the absence of thoracic fovea, and a peculiar disposition of the PMS minor ampullate gland spigots, at the posterior end of the spinning field, and by the transition to a claw tuft made of pseudotenent setae (table 26). This is coincident with Benjamin's (2011: char. 69, "claw tufts with a pointed end") findings, although my scorings are different from his. Here *Aphantochilus* is scored as having true tenent setae (visible in Benjamin's fig. 7H of *A. taurifrons*), in fact, the only documented transition from pseudotenent to tenent (fig. 163B). *Borboropactus*, *Xysticus*, and *Thomisus* are here scored as not having a claw tuft; although the morphology of the setae is similar, they lack the expanded tips on the setal barbs that produce their function. I was not able to distinguish the other types of claw tuft setae scored by Benjamin ("brush," and "*Onomastus*" type).

HIGHER THOMISIDS: The clade 320, here informally labeled as "higher thomisids," is roughly equivalent to the *Thomisus* clade in Benjamin (2011), but including *Boliscus* (Bominae), not represented in that analysis. The higher thomisids comprise most of the species diversity of the family, and have a rather uniform morphology, with characteristic male palpal conformation, including a disk-shaped tegulum (char. 11 in Benjamin, 2011, not scored here) and a hook-shaped ventral tibial apophysis, which seems to have appeared as a guiding mechanism that acts during hematodochal expansion and rotation (Huber, 1994; char. 320). Higher thomisids also have a peculiar cheliceral conformation, with a short fang and a pronounced mound on the promargin (char. 56), and a reduction of the cheliceral teeth, only relictually present in *Boliscus* (Bominae), but totally absent in

TABLE 26
Synapomorphies of Thomisidae and internal clades
See figure 215A for clades, and table 11 for conventions.

RI	**Thomisidae, Clade 315**
0.45	thoracic fovea [0]: present → absent
0.29	cheliceral retromarginal teeth insertion [49]: distinct → on common base
0.55	scales [157]: present → absent
0.71	claw tuft [163]: of tenent setae with widened tip → of pseudotenent setae with acute tip
0.71	claw tuft insertion [173]: delimited plate separated by soft area from lateral cuticle → continuous with lateral cuticle
0.54	epiandrous spigots [214]: present → absent
0.80	minor ampullate on posterior median margin, posterior to the group of aciniforms [275]: absent → present
	Clade 316
0.67	female palpal tarsus apical tenent tuft [79]: absent → of pseudotenent setae
	Clade 317
0.33	superior tarsal claws I teeth symmetry [139]: both claws similar → retroclaw many fewer teeth
0.55	scales [157]: absent → present
0.55	cymbium dorsal chemosensory patch [324]: absent → present
0.48	median apophysis [356]: absent → present
	Clade 318
0.67	tarsal scopula of tenent setae [161]: present → absent
0.50	tarsal trichobothria distribution [189]: all along tarsus → apical field close to tarsal organ
0.49	embolus attachment [351]: flexibly attached → fixed
	Clade 319
0.29	cheliceral retromarginal teeth insertion [49]: on common base → distinct
0.22	superior tarsal claw teeth insertion line [141]: median line → ectal line
0.43	scale axis flattened [158]: axis cylindrical → axis or entire scale flattened
0.31	trichobothria proximal and distal plate limit [176]: well differentiated → homogeneous
0.38	trichobothria proximal plate transverse ridges [178]: with transverse ridges → smooth
0.32	trichobothria distal plate transverse ridge [182]: distal plate embedded below transverse ridge → absent
1.00	crypsis with fungi [390]: absent → present
	Higher thomisids, Clade 320
0.75	lateral eyes on individual bulbous tubercles [7]: absent → present
0.67	cheliceral promarginal pronounced mound [56]: absent → present
0.82	tarsal trichobothria rows [190]: two or three rows → single row
0.59	male palp tibia ventral apical process [320]: absent or simple swelling or part of RTA → present
	Clade 321
0.53	cheliceral promarginal teeth [47]: present → absent
0.44	cheliceral retromarginal teeth [48]: present → absent
0.65	endites obliquely depressed [70]: absent → present
0.31	trichobothria proximal and distal plate limit [176]: well differentiated → not well differentiated
0.44	RTA apical internal file [314]: present → absent
0.75	crypsis through detritus adhesion [389]: present → absent
	Clade 322
0.60	dorsal scutum on male abdomen [205]: absent → present
	Clade 323
0.38	trichobothria proximal plate transverse ridges [178]: with transverse ridges → smooth
0.50	tarsal trichobothria distribution [189]: apical field close to tarsal organ → all along tarsus
0.20	cymbial retromedian process [336]: absent → present without furrow
	Clade 324
0.41	chilum [30]: present → absent
1.00	cheliceral retromarginal pronounced mound [57]: absent → present, with brush of setae
0.65	endites obliquely depressed [70]: present → absent
0.50	endite ventral distal macrosetae [71]: absent → present on distal half
0.22	superior tarsal claw teeth insertion line [141]: median line → mesal line
0.44	male epigastric sclerite [207]: absent → present
1.00	ant shielding behavior [392]: absent → present

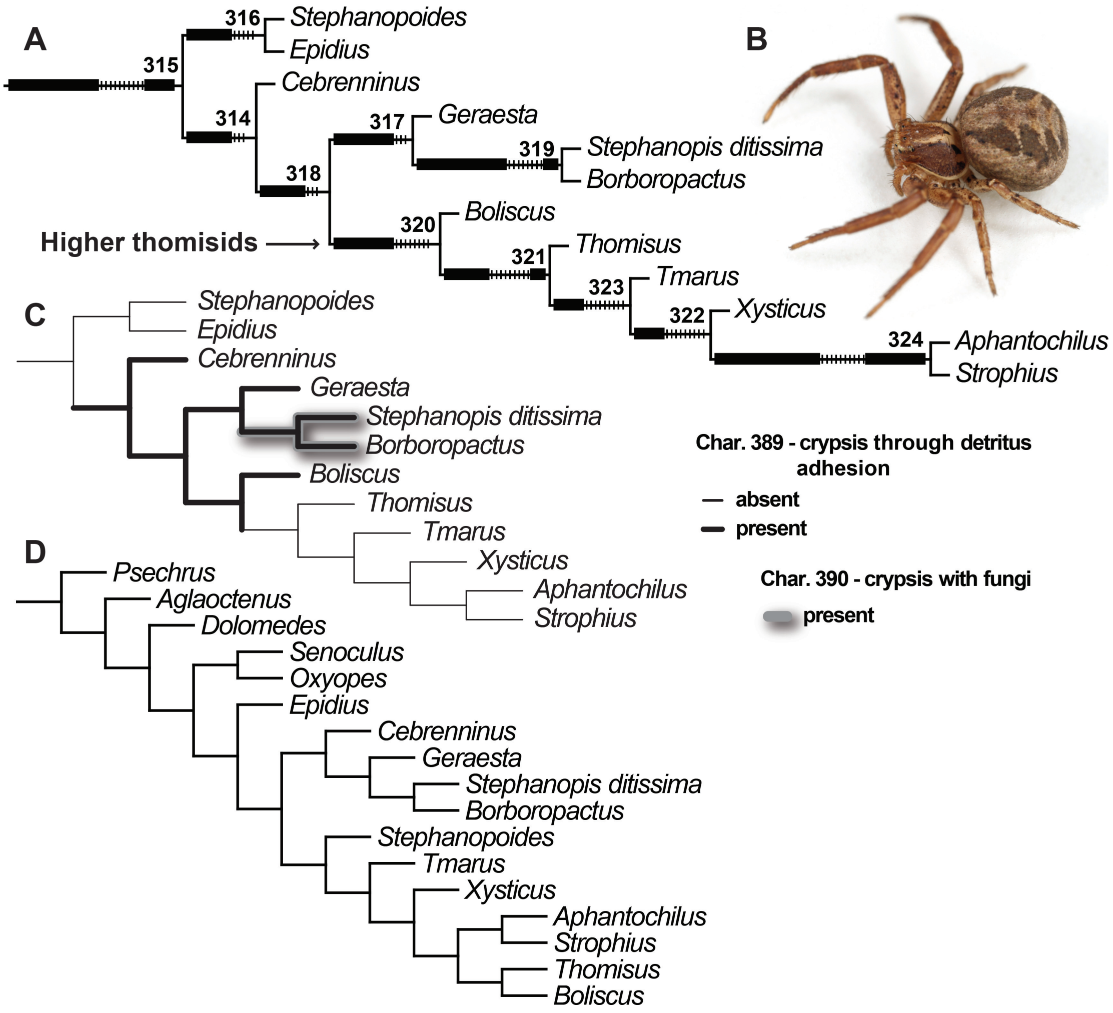

A
315
316
Stephanopoides
Epidius
314
Cebrenninus
318
317
Geraesta
319
Stephanopis ditissima
Borboropactus
Higher thomisids
320
Boliscus
321
Thomisus
323
Tmarus
322
Xysticus
324
Aphantochilus
Strophius
B
C
Stephanopoides
Epidius
Cebrenninus
Geraesta
Stephanopis ditissima
Borboropactus
Boliscus
Thomisus
Tmarus
Xysticus
Aphantochilus
Strophius
Char. 389 - crypsis through detritus adhesion
absent
present
Char. 390 - crypsis with fungi
present
D
Psechrus
Aglaoctenus
Dolomedes
Senoculus
Oxyopes
Epidius
Cebrenninus
Geraesta
Stephanopis ditissima
Borboropactus
Stephanopoides
Tmarus
Xysticus
Aphantochilus
Strophius
Thomisus
Boliscus

Fig. 215. **A.** Cladogram of Thomisidae. **B.** *Xysticus cristatus* female (photo, Stefan Sollfors). **C.** Optimization of the mechanisms of adhesion of detritus to the exoskeleton found in Thomisidae. **D.** Alternative tree of Thomisidae constrained as a member of Lycosoidea s.s. (see table 27).

clade 321. This morphology is correlated with the iconic behavior of consuming their prey through small holes, without chewing their exoskeletons (Foelix, 2011). *Aphantochilus* and *Strophius* appear as sister groups, united, among others, by peculiar modifications of the mouthparts (as hypothesized by Ono, 1988: 223), and the stereotyped behavior of shielding themselves with the exoskeleton of a consumed ant prey (char. 392, fig. 217). *Aphantochilus* is the only instance in this dataset where true tenent setae are developed as a transformation from pseudotenent ones (fig. 198B).

"STEPHANOPINAE": In this analysis, the relationships among the basal thomisids are weakly supported and unstable upon changes in weighting parameters. The monophyly of "Stephanopinae" (i.e., most thomisids retaining cheliceral teeth, here represented by *Cebrenninus*, *Epidius*, *Geraesta*, *Borboropactus*, *Stephanopis ditissima*, and *Stephanopoides*) would be slightly suboptimal, but without a signficant gain in character fit (FD = 2.56, C/F = 1.32). Constraining the monophyly of the *Epidius* group as found in Benjamin (2011; here represented by *Epidius*, *Cebrenninus*, *Geraesta*, and *Borboropactus*) is

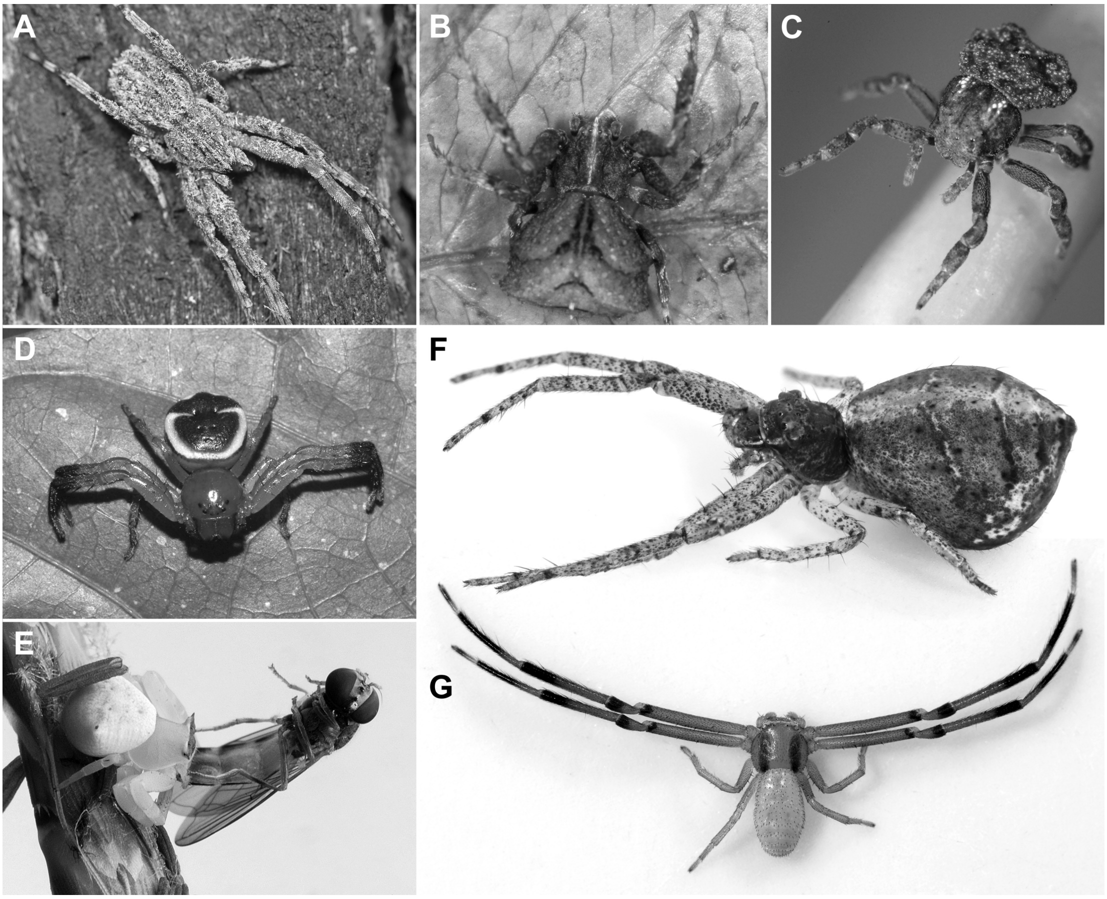


Fig. 216. Representatives of Thomisidae, habitus. **A.** *Stephanopis* cf. *cambridgei* female (photo, Marshal Hedin). **B.** *Stephanopis ditissima* female. **C.** *Boliscus tuberculata* female (photo, Yixiong Cai). **D.** *Stephanopoides* sp. female (photo, Arthur Anker, UFC, Fortaleza, Brazil). **E.** *Thomisus* sp. female (photo, Yixiong Cai). **F.** *Tmarus piger* female (photo, Arno Grabolle). **G.** *Runcinia grammica* female (photo, Arno Grabolle).

far suboptimal for this dataset (FD = 18.51, C/F = 1.46). Most members of "Stephanopinae" are rugose and cryptic, and many of them carry detritus on their bodies (chars. 389, 390). Thomisids use a variety of mechanisms to retain detritus, such as the passive retention of soil crystals (fig. 185C), some sort of viscid fluid (fig. 185F), and fungus hyphae (char. 390; fig. 185H). The two representatives included here that grow fungi on their bodies (*Borboropactus bituberculatus*, from South East Asia, and *Stephanopis ditissima*, from Chile) are joined by several synapomorphies, thus suggesting a monophyletic origin of the association (fig. 215C). The general condition of crypsis by sticking detritus to the exoskeleton is likely homoplasious in thomisids, with a reversal in this analysis, or three independent gains if optimized on the tree of Benjamin (2011). This is not surprising, considering the many convergent acquisitions of similar conditions in other spider families, such as Pisauridae (*Bradystichus*), Zodariidae (*Cryptothele*), Homalonychidae, Sicariidae (*Sicarius*), Microstigmatidae (*Microstigmata*), and Paratropididae (see Duncan et al., 2007; Platnick and Forster, 1993). The placing of *Borboropactus*, well nested inside Thomisidae, seems counterintuitive based on certain

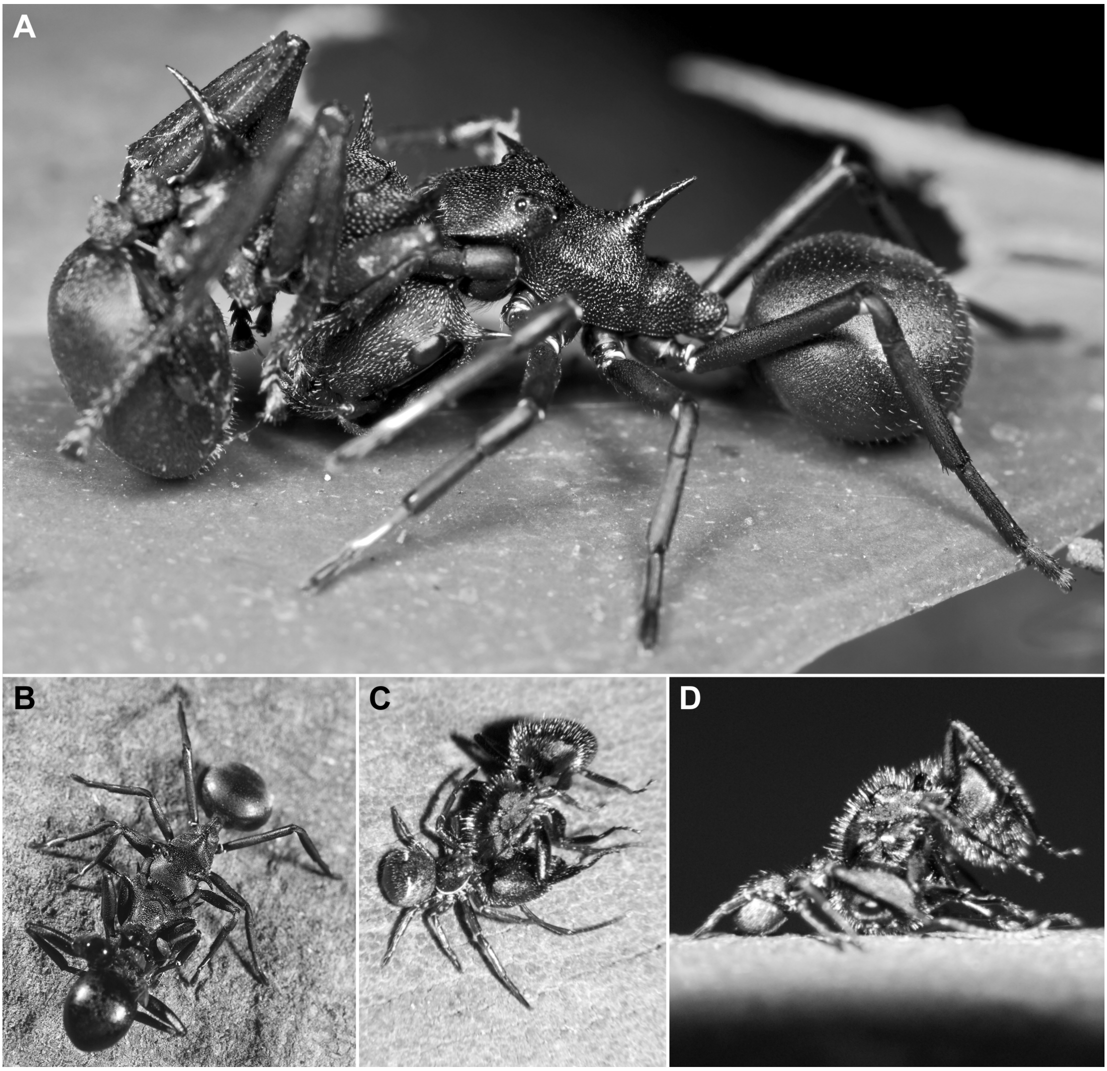


Fig. 217. Ant-shielding behavior of Aphantochilinae and Strophiinae (Thomisidae; character 392). **A.** *Aphantochilus rogersi* (photo, Paul Bertner). **B.** Same (photo, Arthur Anker, UFC, Fortaleza, Brazil). **C, D.** *Strophius* sp. (photos, Gonzalo Rubio).

character systems. The male copulatory bulb has a retrolaterally placed median apophysis and a hyaline conductor, quite standard for the RTA clade, but, unlike other thomisids and as mentioned above, the tapeta are canoe, instead of grate shaped. In this analysis, the tapetum morphology is not of much influence for the placement of *Borboropactus*, as the closest putative relatives have lost their tapeta (Salticidae, Philodromidae) or have a grate morphology (in an alternative placement among higher lycosoids).

ALTERNATIVE AFFILIATION OF THOMISIDAE IN LYCOSOIDEA: During the development of this dataset, several versions resulted in Thomisidae arising from the higher lycosoids, specifically close to Senoculidae and Oxyopidae (fig. 215D). Experiment 8 (see table 3) on ordered characters also produced this grouping. Such a resolution is supported by, among other characters, the peculiar posterior placement of the minor ampullate gland spigots (char. 275) and the posterior eye tapeta, grate shaped in all the

TABLE 27

Character fit variation for alternative placement of Thomisidae in Lycosoidea, s.s.

Individual contribution of variations in fit from each character for the alternative resolution of figure 215D (FD = 15.51, C/F = 1.33). See figure 206 for conventions and Phylogenetic Analysis Methodology.

(c) inferior tarsal claw I size [134] = 20.00
(c) male palp tibia ventral apical process [320] = 6.25
(c) female palpal tarsus apical tenent tuft [79] = 5.77
(c) epiandrous spigots disposition [215] = 3.75
(c) cheliceral promarginal teeth [47] = 3.31
(c) female palpal tarsus dorsal chemosensory setae distribution [83] = 3.31
(c) RTA position [312] = 3.31
(c) metatarsal trichobothria rows [188] = 2.47
…
(f) conductor [359] = −1.65
(f) PLS cylindrical gland spigots, number [295] = −2.02
(f) sternum texture [92] = −2.37
(f) tarsal trichobothria rows [190] = −2.37
(f) ALE tapetum type [22] = −4.09
(f) PME tapetum type [25] = −4.09
(f) endite dorsal setae [73] = −4.95
(f) minor ampullate on posterior median margin, posterior to the group of aciniforms [275] = −6.82
(f) trichobothria distal plate transverse ridge [182] = −8.18

thomisid representatives except *Borboropactus*, which has canoe-shaped tapeta (see table 27). A constrained analysis forcing also philodromids and salticids as lycosoids is furthermore suboptimal (FD = 33.97, C/F = 1.67).

SALTICIDAE

Salticidae appears well supported, although not so strongly as one would expect for such a charismatic group (fig. 218). In fact, apart from certain characters relating to their peculiar eyes, the list of salticid synapomorphies is rather unimpressive (table 28). Salticid monophyly, however, still holds after inactivation of the eye characters. The color reflection of anterior eyes (char. 15), seemingly an antireflex coating, appears as a new character supporting Salticidae, although it is absent in *Lyssomanes*.

The relationships of the basal branches of Salticidae have been elusive in the recent phylogenetic analyses using molecular data (Maddison and Hedin, 2003; Maddison and Needham, 2006). The results obtained here from a small taxon sampling are in some ways similar to those results. *Hispo* (Hisponinae) appears close to *Plexippus* (Salticoida), as most of the molecular evidence suggests (Maddison and Needham 2006: 48; but see Maddison et al., 2008). The asymmetrical tarsal claws, with many more teeth on the proclaw (char. 139), proposed as a synapomorphy for Salticoida, is here also found in *Hispo* and *Holcolaetis* (as well as in several other taxa, mainly scattered among thomisids and philodromids).

Salticoida is here represented only by *Plexippus*, and its autapomorphies are largely coincident with the synapomorphies proposed for that group (Maddison, 1996; Maddison and Hedin, 2003), including the reduction of the palpal claw (fig. 219) and the intercheliceral sclerite, and the well-developed tracheal system (fig. 209). The basal posterior membranous mound on the chelicerae (char. 35) is here also found scattered in several groups (some higher lycosoids, philodromids, a miturgid, a thomisid, etc.). Several characters in the retinal ultrastructure might be additional synapomorphies of Salticoida, although the taxon sampling is logically limited to a few genera (see references in Maddison and Hedin, 2003; Hill and Richman, 2009).

The spartaeines *Portia* and *Holcolaetis* are joined together, but only circumstantially supported by a very homoplasious character (char. 108). The grouping of lyssomanines with spartaeines found in molecular studies does not gain any character support from this

TABLE 28
Synapomorphies of Salticidae and internal clades
See figure 218 for clades, and table 11 for conventions.

RI	**Salticidae (Clade 327)**
0.49	posterior eye row curvature [10]: approximately straight → notably recurved
1.00	AME cone length [14]: short cone or sphere → long cone
0.72	leg orientation [97]: laterigrade → prograde
0.52	cylindrical gland spigots [280]: present → absent
(0.48)	median apophysis [356]: absent → present
	Clade 325
(0.22)	superior tarsal claw teeth insertion line [141]: median line → ectal line
(0.14)	fertilization duct position [379]: posterior → well advanced
	Clade 326
(0.80)	AME-ALE reflection of white light [15]: white reflection → color reflection
(0.59)	conductor sclerotization [360]: hyaline or membranous → sclerotized
	Clade 329
(0.33)	PME vestigial [18]: well developed → very small, vestigial
0.29	palpal claw [85]: present → reduced to nubbin
0.33	superior tarsal claws I teeth symmetry [139]: both claws similar → retroclaw many fewer teeth
0.24	conductor [359]: present → absent
	***Plexippus* (Salticoida)**
0.20	cheliceral basal posterior membranous mound [35]: absent → present
0.00	intercheliceral sclerite [64]: present → absent
0.29	palpal claw [85]: reduced to nubbin → absent
(0.67)	tarsal scopula of tenent setae [161]: present → absent
0.32	trichobothria distal plate transverse ridge [182]: distal plate embedded below transverse ridge → absent
0.60	dorsal scutum on male abdomen [205]: absent → present
0.62	lateral tracheae branching [220]: simple, linear → branched
0.59	median tracheae branching [225]: unbranched → strongly branched
0.62	median tracheae passing to carapace [226]: limited to abdomen → two large trunks with many ramifications passing to carapace
0.36	male PMS minor ampullates, number [274]: one plus nubbin → one no nubbin
0.55	cymbium dorsal chemosensory patch [324]: present → absent
0.48	median apophysis [356]: present → absent

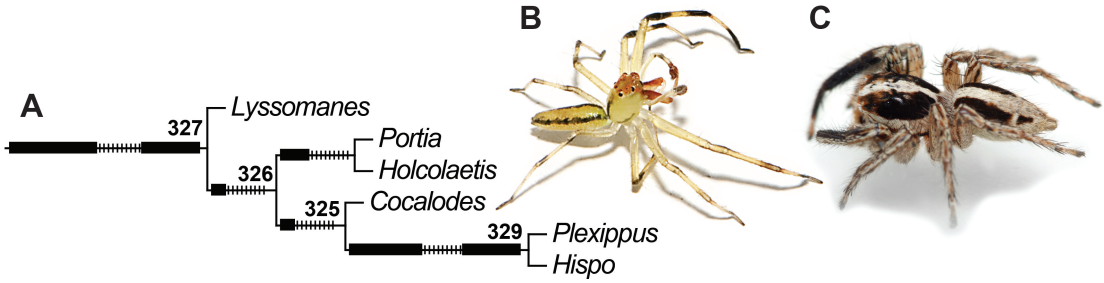


Fig. 218. **A.** Cladogram of Salticidae. **B.** *Lyssomanes viridis* male (photo, Seig Kopinitz), note the overflexion of the tarsus-metatarsus articulation on left legs I and II (see character 121). **C.** *Plexippus paykulli* female (photo, Stefan Sollfors).

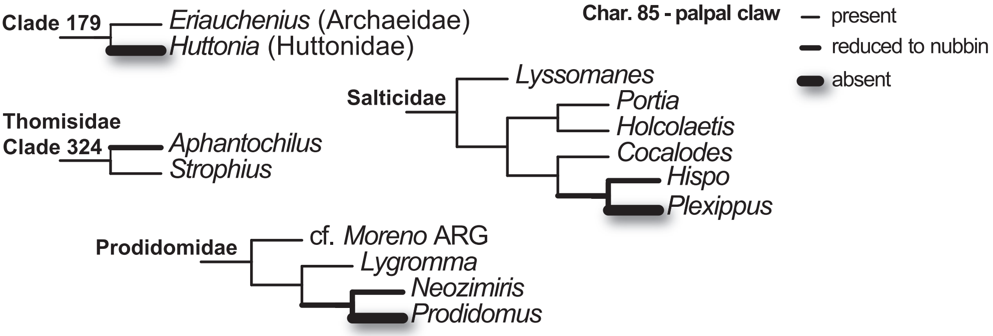

Clade 179
Eriauchenius (Archaeidae)
Huttonia (Huttonidae)
Thomisidae
Clade 324
Aphantochilus
Strophius
Prodidomidae
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus
Salticidae
Lyssomanes
Portia
Holcolaetis
Cocalodes
Hispo
Plexippus
Char. 85 - palpal claw
present
reduced to nubbin
absent

Fig. 219. Reduction and loss of the palpal claw. In this dataset, the two losses documented in Dionycha proceeded through an intermediate relictual claw.

dataset when constrained for monophyly, and lacks synapomorphies (FD = 9.37).

The Oblique Median Tapetum (OMT) Clade

In this analysis, gnaphosoid spiders appear mixed with several other groups, usually placed among corinnids or liocranids. Those groups tend to have the characteristically depressed endites of gnaphosoids, and bright, pale PME. On close examination, the PME tapeta are unlike those of other spiders: their middle dark lines are orthogonal to each other (see comments under char. 26), a disposition that Homann (1971) already referred to as "gnaphosid." A large group with such tapetum orientation, including gnaphosoids, is referred here as the Oblique Median Tapetum (OMT) clade (fig. 220, table 29). That orientation, which allows the tapeta to function as a polarized-light compass, as demonstrated by Dacke et al. (1999) for *Drassodes cupreus*, might be more extended in the OMT clade, although other gnaphosids with a similar morphology do not polarize the light in the same way (Dacke et al., 2001). In this analysis, a basal clade of three trochanteriids (clade 281, fig. 220) is heterogeneous in PME tapetum orientation (fig. 221A), and its placement in the tree is sensitive to weighting regimes. These may as

TABLE 29

Synapomorphies of the OMT and CTC clades and internal clade 232

See figure 220A for clades, and table 11 for conventions.

RI	**OMT Clade (Clade 233)**
0.94	claw tuft seta base thickness [165]: thin base → thick base
0.50	female major ampullate shaft sizes [254]: both similar size → anterior much smaller than posterior
(0.42)	major ampullates, number in male [258]: one plus nubbin → two
(0.68)	demarcation between major ampullate and piriform fields [264]: major ampullate field integrated with piriform field or no furrow → separated by deep furrow male and female
(0.53)	PMS cylindrical gland spigots, number [283]: 3 → 5, or 4
0.81	PMS cylindrical spigots, clustering [284]: mixed with aciniforms or minor ampullates → isolated posterior group
	Clade 232
0.89	PME tapeta symmetry axes [26]: parallel → orthogonal
0.65	endites obliquely depressed [70]: absent → present
(0.67)	tarsal cuticle texture [100]: fingerprint → smooth
	The CTC Clade, 229
0.88	claw–claw tuft clasping mechanism [169]: absent → present
0.50	female major ampullate shaft sizes [254]: anterior much smaller than posterior → both similar size
0.55	cymbium dorsal chemosensory patch [324]: present → absent

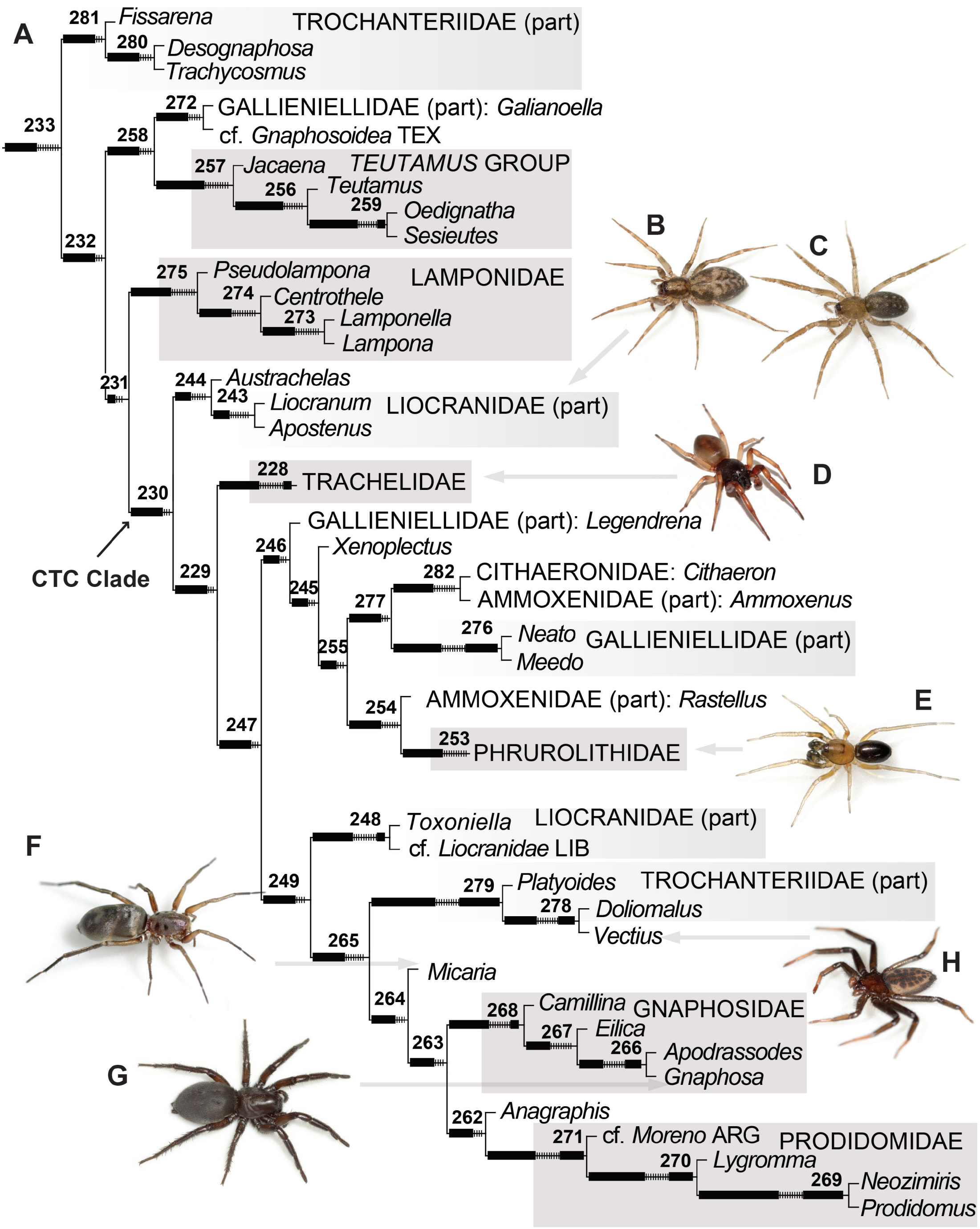

A
281 Fissarena
TROCHANTERIIDAE (part)
280 Desognaphosa
Trachycosmus
233
272 GALLIENIELLIDAE (part): Galianoella
cf. Gnaphosoidea TEX
258
257 Jacaena
TEUTAMUS GROUP
256 Teutamus
259 Oedignatha
Sesieutes
232
275 Pseudolampona
LAMPONIDAE
274 Centrothele
273 Lamponella
Lampona
231
244 Austrachelas
243 Liocranum
LIOCRANIDAE (part)
Apostenus
228 TRACHELIDAE
230
CTC Clade
229
GALLIENIELLIDAE (part): Legendrena
246
Xenoplectus
245
282 CITHAERONIDAE: Cithaeron
AMMOXENIDAE (part): Ammoxenus
277
276 Neato
GALLIENIELLIDAE (part)
Meedo
255
254 AMMOXENIDAE (part): Rastellus
253 PHRUROLITHIDAE
247
248 Toxoniella
LIOCRANIDAE (part)
cf. Liocranidae LIB
249
279 Platyoides
TROCHANTERIIDAE (part)
278 Doliomalus
Vectius
265
Micaria
264
268 Camillina
GNAPHOSIDAE
267 Eilica
266 Apodrassodes
Gnaphosa
263
262 Anagraphis
271 cf. Moreno ARG
PRODIDOMIDAE
270 Lygromma
269 Neozimiris
Prodidomus
B
C
D
E
F
G
H

Fig. 220. **A.** Cladogram of the Oblique Median Tapetum (OMT) clade. **B.** *Liocranum rupicola* (Liocranidae). **C.** *Apostenus fuscus* (Liocranidae). **D.** *Trachelas volutus* (Trachelidae). **E.** *Phrurolithus minimus* (Phrurolithidae). **F.** *Micaria fulgens* (Gnaphosidae, Micariinae). **G.** *Gnaphosa lucifuga* (Gnaphosidae). **H.** *Vectius niger* (Gnaphosidae). (D, photo, Joseph T. Lapp; H, M. Ramírez; all the rest, Arno Grabolle).

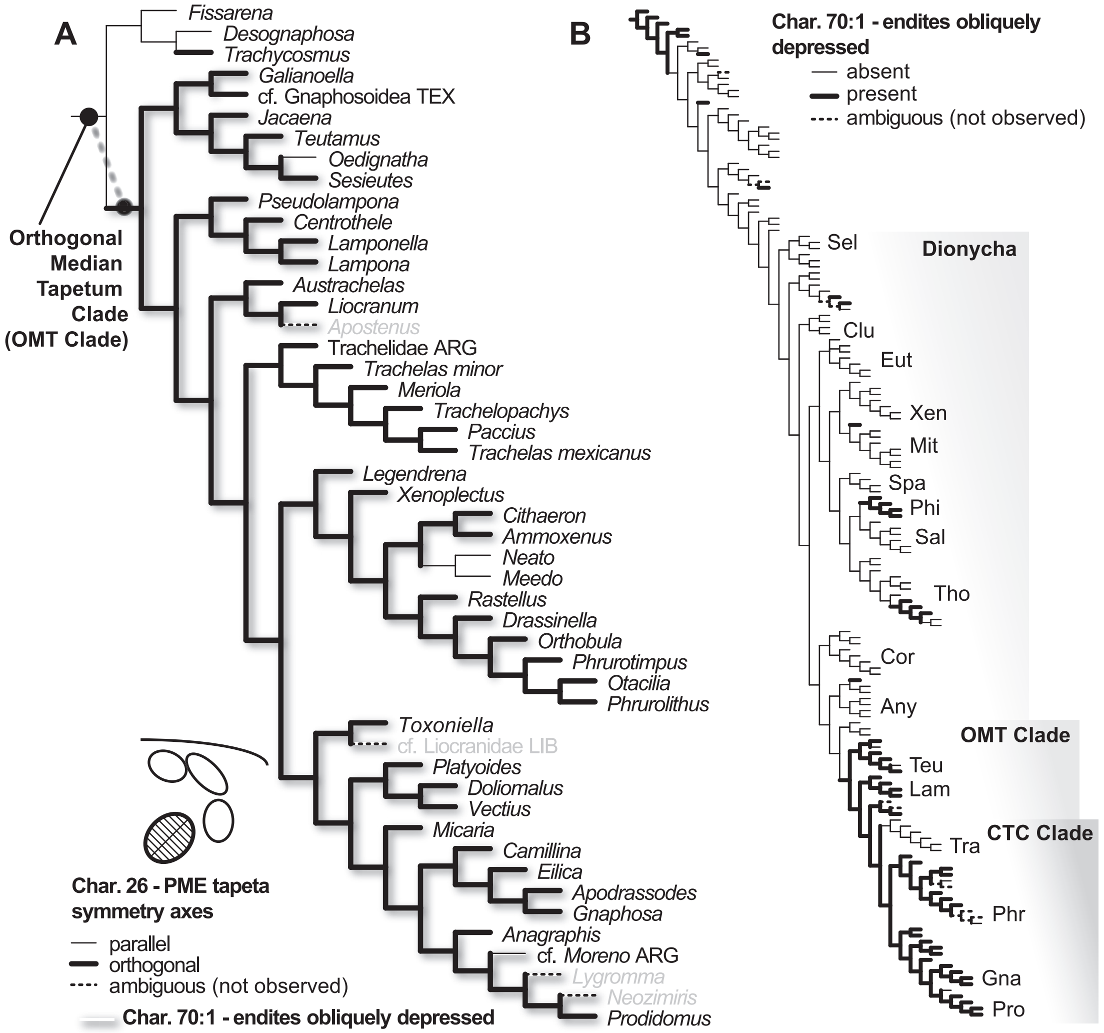

A
Fissarena
Desognaphosa
Trachycosmus
Galianoella
cf. Gnaphosoidea TEX
Jacaena
Teutamus
Oedignatha
Sesieutes
Pseudolampona
Centrothele
Lamponella
Lampona
Austrachelas
Liocranum
Apostenus
Trachelidae ARG
Trachelas minor
Meriola
Trachelopachys
Paccius
Trachelas mexicanus
Legendrena
Xenoplectus
Cithaeron
Ammoxenus
Neato
Meedo
Rastellus
Drassinella
Orthobula
Phrurotimpus
Otacilia
Phrurolithus
Toxoniella
cf. Liocranidae LIB
Platyoides
Doliomalus
Vectius
Micaria
Camillina
Eilica
Apodrassodes
Gnaphosa
Anagraphis
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus
Orthogonal Median Tapetum Clade (OMT Clade)
Char. 26 - PME tapeta symmetry axes
parallel
orthogonal
ambiguous (not observed)
Char. 70:1 - endites obliquely depressed
B
Char. 70:1 - endites obliquely depressed
absent
present
ambiguous (not observed)
Sel
Dionycha
Clu
Eut
Xen
Mit
Spa
Phi
Sal
Tho
Cor
Any
OMT Clade
Teu
Lam
Tra
CTC Clade
Phr
Gna
Pro

Fig. 221. **A.** The orthogonal PME tapeta define a clade of gnaphosoids and other groups usually placed in Liocranidae and Corinnidae, approximately coincident with the optimization of the obliquely depressed endites. **B.** Bird's eye view mapping of the obliquely depressed endites in the entire tree, showing several instances of homoplasy.

well be members of the OMT clade, a possibility that should be tested with a denser sampling of trochanteriids and "liocranids." The depressed endites, a classical character used for gnaphosoids, are also a synapomorphy of this clade, with some homoplasy in several parts of the tree (fig. 221B).

In his seminal work on spigots of gnaphosoids, Platnick (1990) uncovered an amazing diversity of morphological characters that served as synapomorphies of large clades (see Platnick, 2002). The most basal families in the group, however, have more generalized spinneret morphology. For example, the ALS involve a suite of traditional characters of gnaphosoids, some liocranids and clubionids, sometimes involving a remarkable sexual dimorphism; this suite seems to have appeared at least three times (fig. 222). Given the wide distribution of the characters from endites and PME tapetum, it is not surprising that in this analysis the basal gnaphosoid

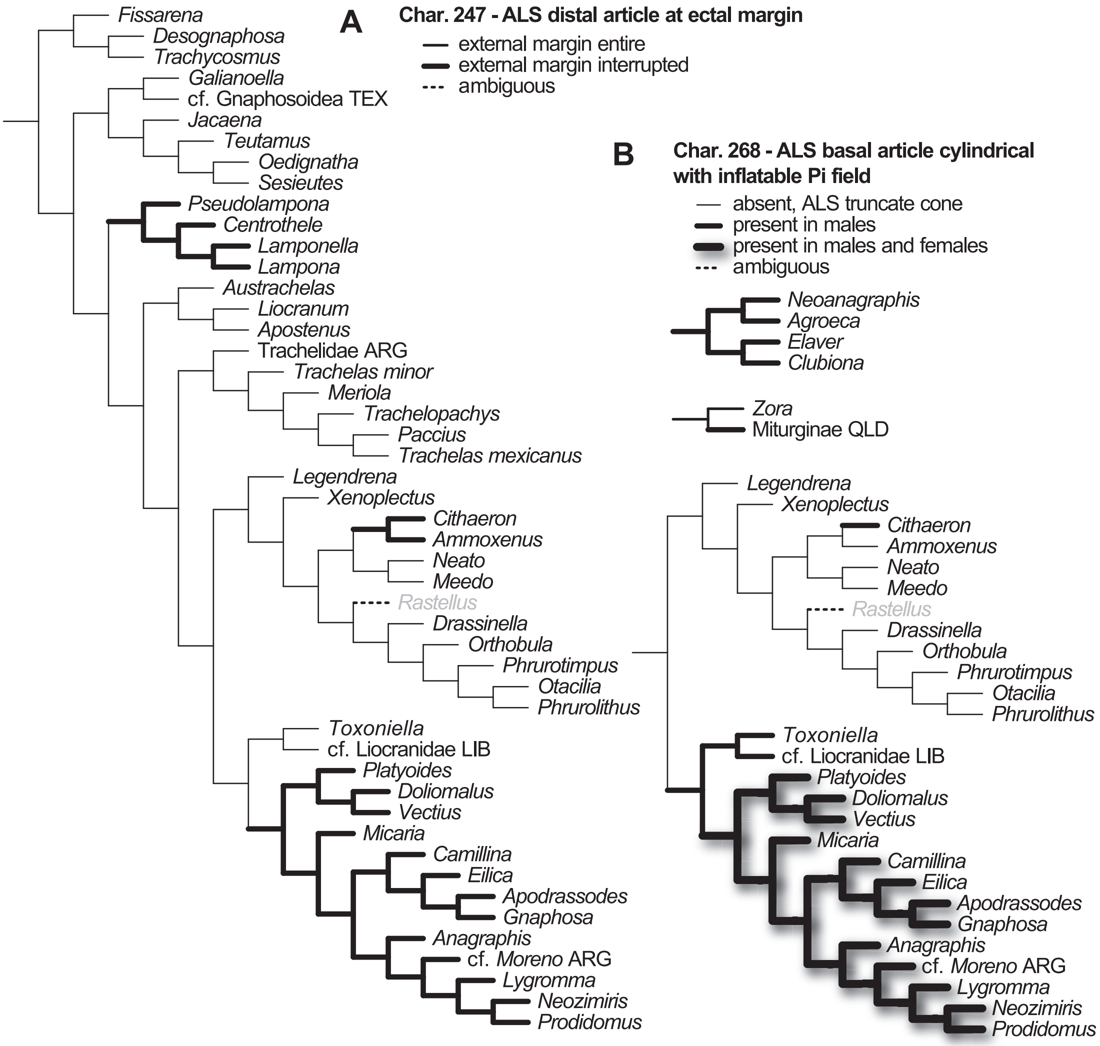

A
Char. 247 - ALS distal article at ectal margin
external margin entire
external margin interrupted
ambiguous
Fissarena
Desognaphosa
Trachycosmus
Galianoella
cf. Gnaphosoidea TEX
Jacaena
Teutamus
Oedignatha
Sesieutes
Pseudolampona
Centrothele
Lamponella
Lampona
Austrachelas
Liocranum
Apostenus
Trachelidae ARG
Trachelas minor
Meriola
Trachelopachys
Paccius
Trachelas mexicanus
Legendrena
Xenoplectus
Cithaeron
Ammoxenus
Neato
Meedo
Rastellus
Drassinella
Orthobula
Phrurotimpus
Otacilia
Phrurolithus
Toxoniella
cf. Liocranidae LIB
Platyoides
Doliomalus
Vectius
Micaria
Camillina
Eilica
Apodrassodes
Gnaphosa
Anagraphis
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus
B
Char. 268 - ALS basal article cylindrical with inflatable Pi field
absent, ALS truncate cone
present in males
present in males and females
ambiguous
Neoanagraphis
Agroeca
Elaver
Clubiona
Zora
Miturginae QLD
Legendrena
Xenoplectus
Cithaeron
Ammoxenus
Neato
Meedo
Rastellus
Drassinella
Orthobula
Phrurotimpus
Otacilia
Phrurolithus
Toxoniella
cf. Liocranidae LIB
Platyoides
Doliomalus
Vectius
Micaria
Camillina
Eilica
Apodrassodes
Gnaphosa
Anagraphis
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus

Fig. 222. **A.** Mapping of the reduction of the terminal ALS article. **B.** Mapping of the inflatable ALS piriform field. The modified male ALS appears at least three times, and becomes constant for all stages in higher gnaphosoids. The inflatable field and the reduction of the terminal article are approximately associated.

groups appear mixed with other members of the OMT clade. A few experiments applying monophyly constraints help dissect the character support in favor of or against the monophyly of gnaphosoids. When they are constrained to be monophyletic, the results are quite suboptimal, without much increase in fit from other characters (fig. 223). As expected, a monophyletic Gnaphosoidea would be favored mainly by characters from the spigots, and mostly opposed by the new characters found here, such as the claw tufts, Bennett's glands, and PME tapetum, but also opposed by several characters from spinnerets and spigots as well (tables S12–14, see supplementary material: http://dx.doi.org/10.5531/sd.sp.4). The Liocranidae is high in the list of the problems left unsolved by the present analysis, even when several terminals probably related to *Liocranum* were included (e.g., *Apostenus*, *Toxoniella*, and cf. Liocranidae LIB). Real progress is made, however,

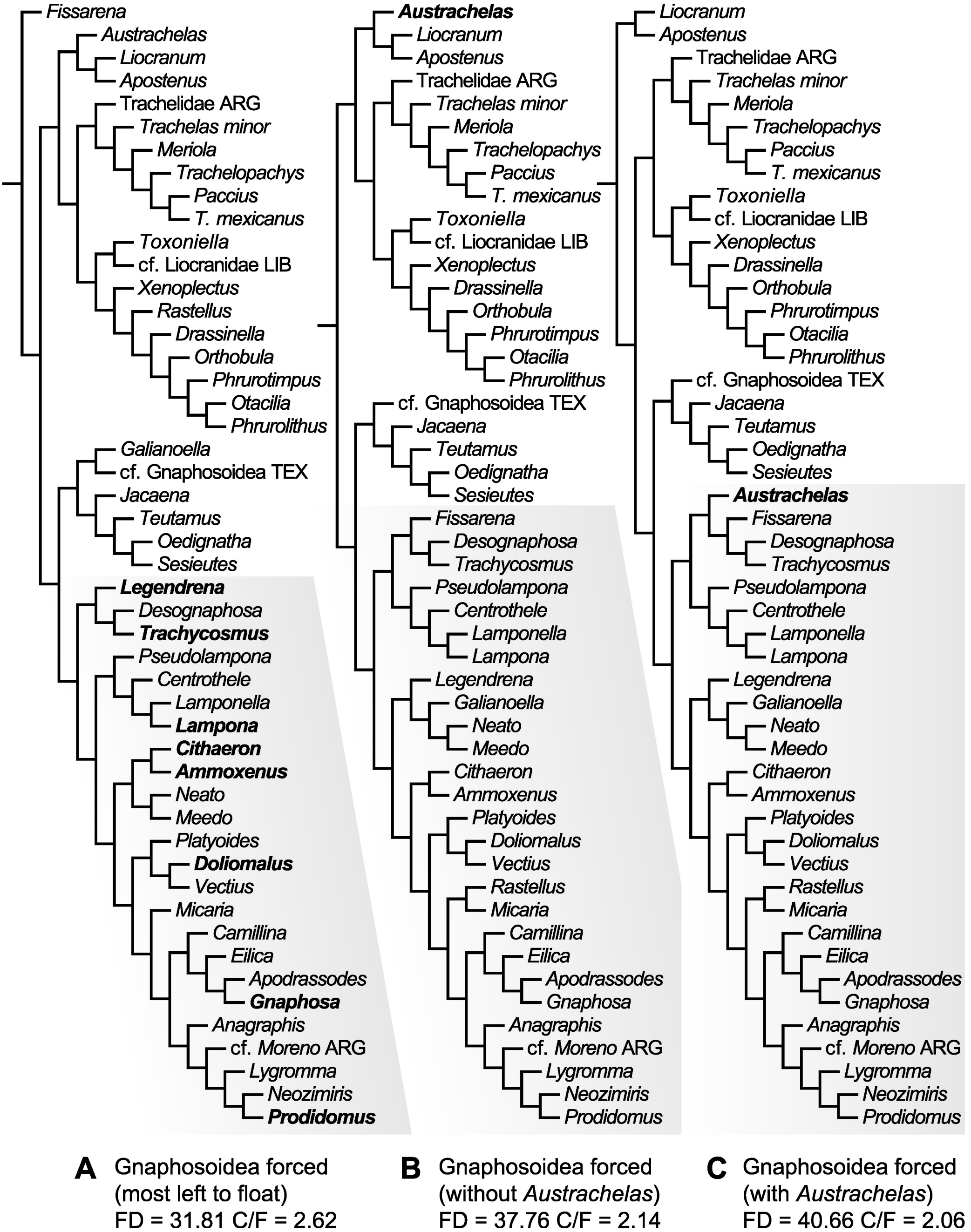

Fissarena
Austrachelas
Liocranum
Apostenus
Trachelidae ARG
Trachelas minor
Meriola
Trachelopachys
Paccius
T. mexicanus
Toxoniella
cf. Liocranidae LIB
Xenoplectus
Rastellus
Drassinella
Orthobula
Phrurotimpus
Otacilia
Phrurolithus
Galianoella
cf. Gnaphosoidea TEX
Jacaena
Teutamus
Oedignatha
Sesieutes
Legendrena
Desognaphosa
Trachycosmus
Pseudolampona
Centrothele
Lamponella
Lampona
Cithaeron
Ammoxenus
Neato
Meedo
Platyoides
Doliomalus
Vectius
Micaria
Camillina
Eilica
Apodrassodes
Gnaphosa
Anagraphis
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus
A Gnaphosoidea forced (most left to float) FD = 31.81 C/F = 2.62
B Gnaphosoidea forced (without Austrachelas) FD = 37.76 C/F = 2.14
C Gnaphosoidea forced (with Austrachelas) FD = 40.66 C/F = 2.06

Fig. 223. Best resolution for Gnaphosoidea (shaded) constrained as monophyletic. **A.** One terminal per family constrained, in boldface, and all other gnaphosoids left to float (FD = 31.81, C/F = 2.62). **B.** All Gnaphosoidea constrained, excluding *Austrachelas* (FD = 37.76, C/F = 2.14). **C.** Same, including *Austrachelas* (FD = 40.66, C/F = 2.06). See tables S13–15 for character fit variation under each resolution.

TABLE 30
Synapomorphies of the *Teutamus* group and internal clades
See figure 220 for clades, and table 11 for conventions.

RI	***Teutamus* group, Clade 257**
0.22	superior tarsal claw teeth insertion line [141]: median line → mesal line
0.43	female epigastric sclerite [203]: absent → present
(0.44)	male epigastric sclerite [207]: absent → present
0.44	male epigastric sclerite surrounding pedicel base [208]: absent → present closed tube
(0.54)	epiandrous spigots [214]: present → absent
0.33	posterior book lungs or modifications [219]: pair of tracheae → absent
0.50	female PMS minor ampullates, number [273]: one plus nubbin → one no nubbin
	Clade 256
0.67	pedicel ventral sclerite–sternum articulation [198]: free → fused
1.00	female epigastric sclerite dorsal surrounding pedicel base [204]: absent → present closed tube
0.59	extension of dorsal scutum on male abdomen [206]: limited to anterior half of abdomen → beyond anterior half of abdomen
	Clade 259
0.33	clypeus margin profile [29]: straight or slightly curved → produced in a median lobe
0.41	chilum [30]: present → absent
0.34	female PMS aciniform spigots, number [276]: 1 → 4 or more
0.25	male PMS aciniform spigots, number [277]: 1 → 2–3
0.53	RTA with canal [316]: canal present → canal absent
	Oedignatha
0.89	PME tapeta symmetry axes [26]: orthogonal → parallel
0.60	promarginal escort seta [52]: present → absent
0.00	intercheliceral sclerite [64]: present → absent
0.65	endites obliquely depressed [70]: present → absent
0.00	fusion of sternum with pleural bars [94]: free → fused
0.66	precoxal triangles in female [95]: fused to sternum → absent
0.22	superior tarsal claw teeth insertion line [141]: mesal line → median line
0.71	claw tuft [163]: absent → of tenent setae with widened tip
0.00	ventral postepigastric scutum [209]: absent → present in male
0.64	colulus [237]: hairy plate or two setae → absent
0.00	spigot shaft surface [240]: longitudinally ridged → smooth
0.00	female major ampullate field invagination [255]: marginal field → central invaginated field transverse line
0.68	demarcation between major ampullate and piriform fields [264]: separated by deep furrow male and female → major ampullate field integrated with piriform field or no furrow
0.53	PMS cylindrical gland spigots, number [283]: many → 5
0.81	PMS cylindrical spigots, clustering [284]: isolated posterior group → mixed with aciniforms or minor ampullates
0.59	PLS cylindrical gland spigots, number [295]: 2 → 1
0.30	RTA sclerotization [315]: with membranous area → all sclerotized
0.53	cymbial trichobothria [329]: present → absent
0.49	embolus attachment [351]: flexibly attached → fixed
0.24	conductor [359]: present → absent

by isolating better-defined clades, such as Trachelidae, Phrurolithidae, and by recognizing the *Teutamus* group (see below).

The *Teutamus* Group

This analysis recovered a monophyletic group of genera with heavily sclerotized body and forelegs armored with a long series of strong macrosetae (clade 257 in fig. 220A; table 30), formerly placed in Phrurolithinae by Deeleman-Reinhold (2001). The male copulatory bulbs of *Sesieutes*, *Jacaena*, and *Teutamus* are all very similar, often with the embolus hidden between the bulb and the cymbium, associated with a longitudinal, grooved conductor (see comments under char. 359). Bonaldo (2000: 137) suggested this association, and Bosselaers and Jocqué also recovered the group (2002: fig. 5, clade

TABLE 31

Synapomorphies of Lamponidae and internal clades

See figure 220 for clades, and table 11 for conventions.

RI	**Lamponidae, Clade 275**
0.53	female palpal tarsus dorsal chemosensory setae distribution [83]: scattered → in a defined patch
(0.47)	spination legs I–II dramatically reduced [143]: with spines → virtually no spines
0.42	spination legs III–IV dramatically reduced [144]: with spines → virtually no spines
(0.44)	male epigastric sclerite [207]: absent → present
0.89	ALS distal article at ectal margin [247]: external margin entire → external margin interrupted
	Clade 273
0.16	anterior eye row curvature [9]: approximately straight → notably procurved
0.54	PME lens curvature [19]: convex → flattened
0.44	cheliceral retromarginal teeth [48]: present → absent
0.36	male PMS minor ampullates, number [274]: one plus nubbin → two
0.49	embolus attachment [351]: flexibly attached → fixed
	Clade 274
0.27	sternum texture [92]: smooth → rugose setal bases raised
0.43	female epigastric sclerite [203]: absent → present
(0.60)	dorsal scutum on male abdomen [205]: absent → present
0.29	postepigastric invaginations [212]: absent → present

28), but it was allied instead to putatively basal corinnids (*Pseudocorinna* and *Pronophaea*, also included in this analysis; fig. 200D). Forcing the *Teutamus* group to be placed together with Phrurolithidae produces moderately suboptimal results (FD = 16.46, C/F = 1.34), with the group sister to Phrurolithidae, joined only by the male dorsal scutum and epigastric sclerite (chars. 205, 207). The genus *Oedignatha* diverges strongly from the otherwise homogeneous group, as evidenced from the extensive list of autapomorphies (table 30), some of them reversals of characters of the OMT clade. As noted above, its inclusion in the *Pronophaea* group recovers a secondary signal from many characters.

LAMPONIDAE

The resolution of Lamponidae in this analysis (fig. 220, table 31) is compatible with the tree obtained by Platnick (2000), even when many of his characters could not be used for this analysis. The groups are well supported and insensitive to changes in weighting parameters. The postepigastric invaginations (char. 212), which are small in Pseudolamponinae (Platnick, 2000: 245), were not found in the only representative included for that subfamily, but appeared scattered in the tree in five unrelated terminals, hence, its low retention index.

THE CLAW TUFT CLASPER (CTC) CLADE

Platnick el al. (2005) discovered a strikingly peculiar claw–claw tuft clasping mechanism made of several claw teeth appressed together and grasping a claw tuft seta (see chars. 169, 170). He proposed that the character may define a small group of prodidomid genera (*Moreno*, *Chilongius*, the undescribed genus cf. *Moreno* ARG, and perhaps *Tricongius*). After a detailed examination on a broad taxonomic scale, it turns out that the clasping mechanism is a synapomorphy of a large group (here named the CTC clade, fig. 220A, table 29), and that the conformation of the clasper as several teeth appressed together occurs as well in some trachelids and gnaphosids (fig. 224). The clasping mechanism, together with the interfolded claw tuft bases may probably work as a means to control the movement of the tenent setae, alternative to the hydraulic movement allowed by a movable claw tuft plate. This is consistent with the phylogenetic distribution of the folded setal bases (fig. 227) and the transition from an articulate to a fixed claw tuft insertion (fig. 198C).

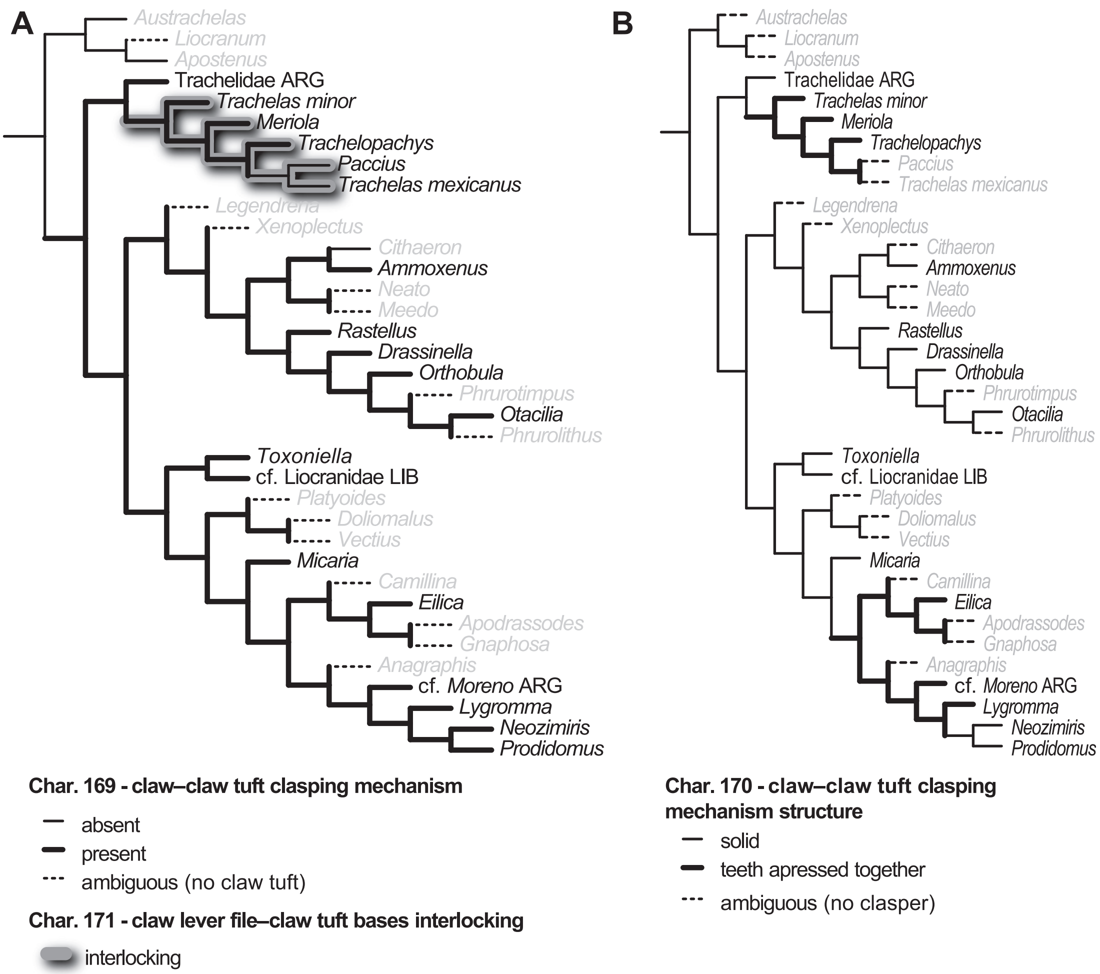

A
Austrachelas
Liocranum
Apostenus
Trachelidae ARG
Trachelas minor
Meriola
Trachelopachys
Paccius
Trachelas mexicanus
Legendrena
Xenoplectus
Cithaeron
Ammoxenus
Neato
Meedo
Rastellus
Drassinella
Orthobula
Phrurotimpus
Otacilia
Phrurolithus
Toxoniella
cf. Liocranidae LIB
Platyoides
Doliomalus
Vectius
Micaria
Camillina
Eilica
Apodrassodes
Gnaphosa
Anagraphis
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus
Char. 169 - claw–claw tuft clasping mechanism
absent
present
ambiguous (no claw tuft)
Char. 171 - claw lever file–claw tuft bases interlocking
interlocking
B
Austrachelas
Liocranum
Apostenus
Trachelidae ARG
Trachelas minor
Meriola
Trachelopachys
Paccius
Trachelas mexicanus
Legendrena
Xenoplectus
Cithaeron
Ammoxenus
Neato
Meedo
Rastellus
Drassinella
Orthobula
Phrurotimpus
Otacilia
Phrurolithus
Toxoniella
cf. Liocranidae LIB
Platyoides
Doliomalus
Vectius
Micaria
Camillina
Eilica
Apodrassodes
Gnaphosa
Anagraphis
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus
Char. 170 - claw–claw tuft clasping mechanism structure
solid
teeth apressed together
ambiguous (no clasper)

Fig. 224. Mapping of claw tuft clasping mechanisms, through hooks at claw base or claw lever file. **A.** A clade of derived Trachelidae seems to have replaced one mechanism by the other (*Paccius* + *Trachelas mexicanus*). **B.** The clasper made of teeth appressed together occurs in two separate clades.

The CTC clade seems at first not especially robust with regard to weighting regimes, as only two of the weighting strengths explored recovered exactly the same group. On a closer inspection, however, the composition of the group changes only by the alternative placement of a few terminals that have lost the claw tufts; the CTC mechanism has a single origin across all weighting regimes, defining roughly the same group. That is, even if the precise taxonomic composition of the CTC clade is not well settled, the evolutionary hypothesis of the origin of the CTC mechanism is better established.

The genera *Toxoniella* and *Xenoplectus*, currently listed in Liocranidae and Gnaphosidae, respectively, as well as the apparently undescribed genus cf. Liocranidae LIB, all lack any of the modifications of the ALS and piriform gland spigots characteristic of those families (fig. 124E). They fit well in the generalized pattern of the CTC clade, and their familial position could be solved after the study of more representatives today placed in Liocranidae. Bosselaers and Jocqué (2013) recently described the African genus *Cteniogaster*, which they placed in Liocranidae. The genus is similar to *Toxoniella* in somatic and genital

TABLE 32

Synapomorphies of Trochanteriidae and related groups

See figure 220 for clades, and table 11 for conventions.

RI	**part of Trochanteriidae, Clade 281**
0.50	ALS separation [243]: contiguous → separate about a diameter or more
0.44	cymbial tip ventral groove [323]: absent → present
0.49	epigynum lobes [365]: lateral lobe and median field delimited by furrows or sutures → undivided plate suture not visible
	Clade 280
0.47	spination legs I–II dramatically reduced [143]: with spines → virtually no spines
(0.55)	scales [157]: present → absent
(0.54)	epiandrous spigots [214]: present → absent
0.33	posterior book lungs or modifications [219]: pair of tracheae → absent
1.00	third entapophyses or median tracheae [222]: present → absent
0.59	PLS cylindrical gland spigots, number [295]: 2 → 1
0.48	median apophysis [356]: present → absent
	part of Trochanteriidae, Clade 279
1.00	carapace flatness [3]: domed or slightly flattened → extremely flat, straight drosal profile
0.29	carapace posterior reflexed border [4]: narrow or not reflexed → wide reflexed border
0.67	PME lens limits [20]: lens raised from surrounding cuticle → lens not raised totally flat
0.50	sternum shape [89]: shield shaped → oval
0.72	leg orientation [97]: prograde → laterigrade
0.47	spination legs I–II dramatically reduced [143]: with spines → virtually no spines
0.42	spination legs III–IV dramatically reduced [144]: with spines → virtually no spines
0.33	femoral dorsal median line macrosetae [146]: present at least one → all absent
0.48	scales setules [159]: present → absent
0.71	claw tuft [163]: of tenent setae with widened tip → absent
0.22	anterior margin of pedicel ventral sclerite [199]: pointed → widely truncate
0.26	cymbial apex extension beyond alveolus [325]: extending beyond distal margin of alveolus → short wide not extending
	Clade 278
0.45	thoracic fovea [0]: present → absent
0.50	position of openings posterior respiratory system [221]: very close to spinnerets → slightly separated from spinnerets
0.64	colulus [237]: hairy plate or two setae → absent
0.50	female PMS minor ampullates, number [273]: two → one no nubbin
0.34	female PMS aciniform spigots, number [276]: 2–3, or 1 → 0
0.53	PMS cylindrical gland spigots, number [283]: 4 → many
0.59	PLS cylindrical gland spigots, number [295]: 2 → 4, or 3
0.15	embolar basal process [352]: absent → present

morphology, and also in having very small posterior median eyes. Their figure of the leg tarsal tip of *Cteniogaster hexomma* (Bosselaers and Jocqué, 2013: fig. 6H) shows a claw tuft of a few tenent setae with their folded bases packed together, and at least one tooth of the claw–claw tuft clasping mechanism. In their analysis, *Agroeca* and *Neoanagraphis*, both lacking the OMT tapetum and the CTC mechanism, are well nested in Liocranidae. A constrained analysis forcing Liocranidae to fit their delimitation is suboptimal for this dataset, and does not show much improvement in fit in other characters (FD = 31.75, C/F = 1.56; table S24, see supplementary data: http://dx.doi.org/10.5531/sd.sp.4).

Trochanteriidae and Allies

In this analysis, the Trochanteriidae is split into two distinct groups, placed among basal or advanced gnaphosoids (fig. 220A, table 32), although the more basal group has low support values and is unstable through weighting regimes. A constrained analysis with trochanteriids forced to be monophyletic is, however, remarkably suboptimal (table S15, see supplementary data: http://dx.doi.

org/10.5531/sd.sp.4). These results are partially due to the interpretation of characters 247 and 268, both describing the ectal margin of the ALS, which is flexible and inflatable in higher gnaphosoids and in clade 279, and by a possible syndrome of characters all correlated with living under bark: flat body and PMS lens, shape of sternum, etc. The two characters that would favor most a monophyletic Trochanteriidae as currently defined (here represented by *Doliomalus*, *Platyoides*, *Fissarena*, *Desognaphosa*, and *Trachycosmus*, without *Vectius*) are the widened piriform gland spigot shafts (char. 262, placing *Vectius* apart, closer to Gnaphosidae), and the clypeus produced in a median lobe (char. 29, joining *Doliomalus* with *Platyoides*, apart from *Vectius*, and thus avoiding one homoplasious step). *Vectius* is remarkably similar to *Doliomalus* in general appearance, and it is unlikely that trochanteriids are split apart only because of a convergent somatic morphology in *Vectius*: a reanalysis of this dataset excluding *Vectius* produced the same results. Similarly, the inclusion of the Asian genus *Plator*, currently listed in Trochanteriidae, should not alter these results, because their spinnerets are very similar to those of *Doliomalus*, and the general body and genital morphology is almost undistinguishable from those of *Vectius* (Platnick, 1976, 1990; Zhu et al., 2006). The placement of *Doliomalus* and *Vectius* depends, however, on the additivity of the characters based on counts, as all experiments 5 through 9 (table 3) resulted in *Doliomalus* sister to *Platyoides*, and these sister to *Vectius* (FD = 4.69, C/F = 1.81).

GALLIENIELLIDAE

Gallieniellids were defined by their tubuliform, paraxial chelicerae (char. 34; see Platnick, 2002). Here the chelicerae of *Drassodella* were not considered to fit the derived gallieniellid shape. This analysis does not recover a monophyletic Gallieniellidae (fig. 220A), although a constrained analysis is slightly suboptimal, with almost as many characters increasing its fit (FD = 2.21, C/F = 1.05) and a resolution compatible with the tree in Platnick (2002). The monophyly of gallieniellids should be tested with a denser sampling, including *Gallieniella*, but unfortunately such a sample was not available at the beginning of this study. In a recent study, Haddad et al. (2009) obtained a tree on which the African genus *Austrachelas* is placed within Gallieniellidae. With this dataset, a constrained analysis obtains a quite suboptimal tree with *Austrachelas* sister to all gallieniellids, without much improvement in other characters (FD = 18.07, C/F = 1.54). I have included one mysterious spider from Texas (cf. Gnaphosoidea TEX) that is currently under study by Norman Platnick and Darrell Ubick. This terminal switched positions across the OMT clade as the study progressed, and the final placement sister to *Galianoella* is not particularly sensible.

TRACHELIDAE

The Trachelidae appears to be well supported, with several synapomorphies, and unsensitive to weighting regimes (fig. 225, table 33). Haddad and Lyle (2008) and Haddad (2006) suggested that the tracheline genera *Poachelas* and *Spinotrachelas* might be the most basal members of the family because they retained fully developed leg spines. They also suggested that genera such as *Fuchiba* and *Fuchibotulus*, which lack both spines and cusps even in males, should be among the most-derived trachelids. This analysis is compatible with a group of basal trachelids bearing leg spines, although Trachelidae ARG lacks cuspules as well. The loss of spination on legs I–II, and III–IV (chars. 143, 144, respectively) are informative for grouping (RI = 0.5 and 0.4, respectively), but quite homoplasious as well (CI = 0.06 and 0.04). A derived group of Trachelidae is here supported by a unique blocklike shape of the claw tuft setae bases (char. 164). Where exactly in the tree this morphology appears is ambiguous, as *Trachelas minor* has an intermediate condition (figs. 227B, 72D–G). In higher trachelines, the expanded setal bases mesh with enlarged ridges in the claw lever. The optimization of another mechanism clasping on the tuft setae (through a hook on the claws, char. 169) suggests that trachelines first had both mechanisms, and

TABLE 33

Synapomorphies of Trachelidae and internal clades

See figure 225A for clades, and table 11 for conventions.

RI	**Trachelidae, Clade 228**
0.65	endites obliquely depressed [70]: present → absent
0.17	palpal claw teeth [86]: one to several teeth → no teeth
0.33	metatarsal preening comb [117]: brush or absent → distinct comb
0.42	spination legs III–IV dramatically reduced [144]: with spines → virtually no spines
0.33	femoral dorsal median line macrosetae [146]: present at least one → all absent
(0.55)	scales [157]: present → absent
(0.54)	epiandrous spigots [214]: present → absent
0.38	major ampullates, number in female [253]: two → one plus nubbin
0.48	median apophysis [356]: present → absent
0.29	secondary spermatheca size, relative to primary spermatheca [373]: smaller than primary spermatheca → about as large as primary spermatheca, or larger than primary spermatheca
	Clade 227
0.47	spination legs I–II dramatically reduced [143]: with spines → virtually no spines
0.60	claw–claw tuft clasping mechanism structure [170]: solid → teeth appressed together
1.00	claw lever file–claw tuft bases interlocking [171]: not interlocking → interlocking
0.60	dorsal scutum on male abdomen [205]: absent → present
0.44	cymbial tip apical thick setae [327]: absent → present
	Clade 235
1.00	female leg cuspules [150]: absent → present
0.60	sexually dimorphic leg macrosetae-cuspules [151]: leg cuspules absent → macrosetae reduced to cuspules in male
0.59	extension of dorsal scutum on male abdomen [206]: limited to anterior half of abdomen → beyond anterior half of abdomen
0.50	female PMS minor ampullates, number [273]: two → one plus nubbin
0.53	PMS cylindrical gland spigots, number [283]: 4 → 5
0.55	cymbium dorsal chemosensory patch [324]: absent → present
	Clade 236
0.17	palpal claw teeth [86]: no teeth → one to several teeth
	Clade 237
0.60	promarginal escort seta [52]: present → absent
0.50	palpal claw apex profile [87]: pointed → truncate
0.88	claw–claw tuft clasping mechanism [169]: present → absent
0.44	male epigastric sclerite surrounding pedicel base [208]: absent → present closed tube
0.54	epiandrous spigots [214]: absent → present
0.49	epigynum lobes [365]: lateral lobe and median field delimited by furrows or sutures → undivided plate suture not visible

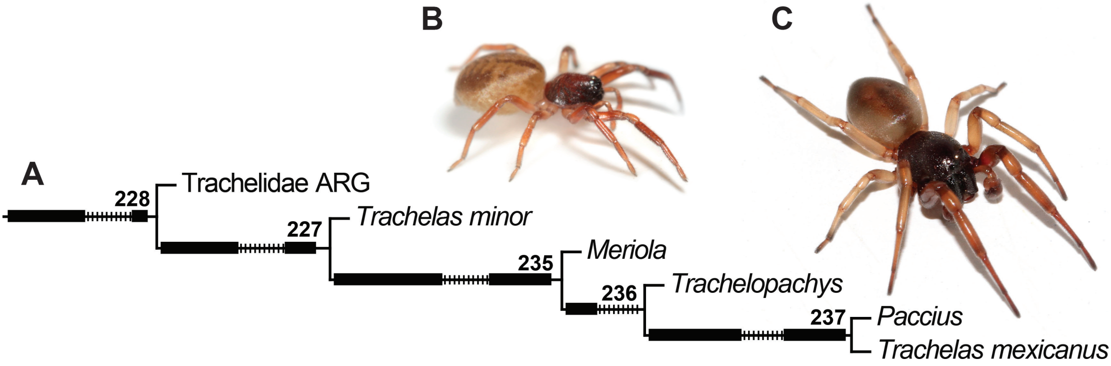


Fig. 225. **A.** Cladogram of Trachelidae. **B.** Trachelidae ARG female. **C.** *Trachelas volutus* (photo, Joseph T. Lapp).

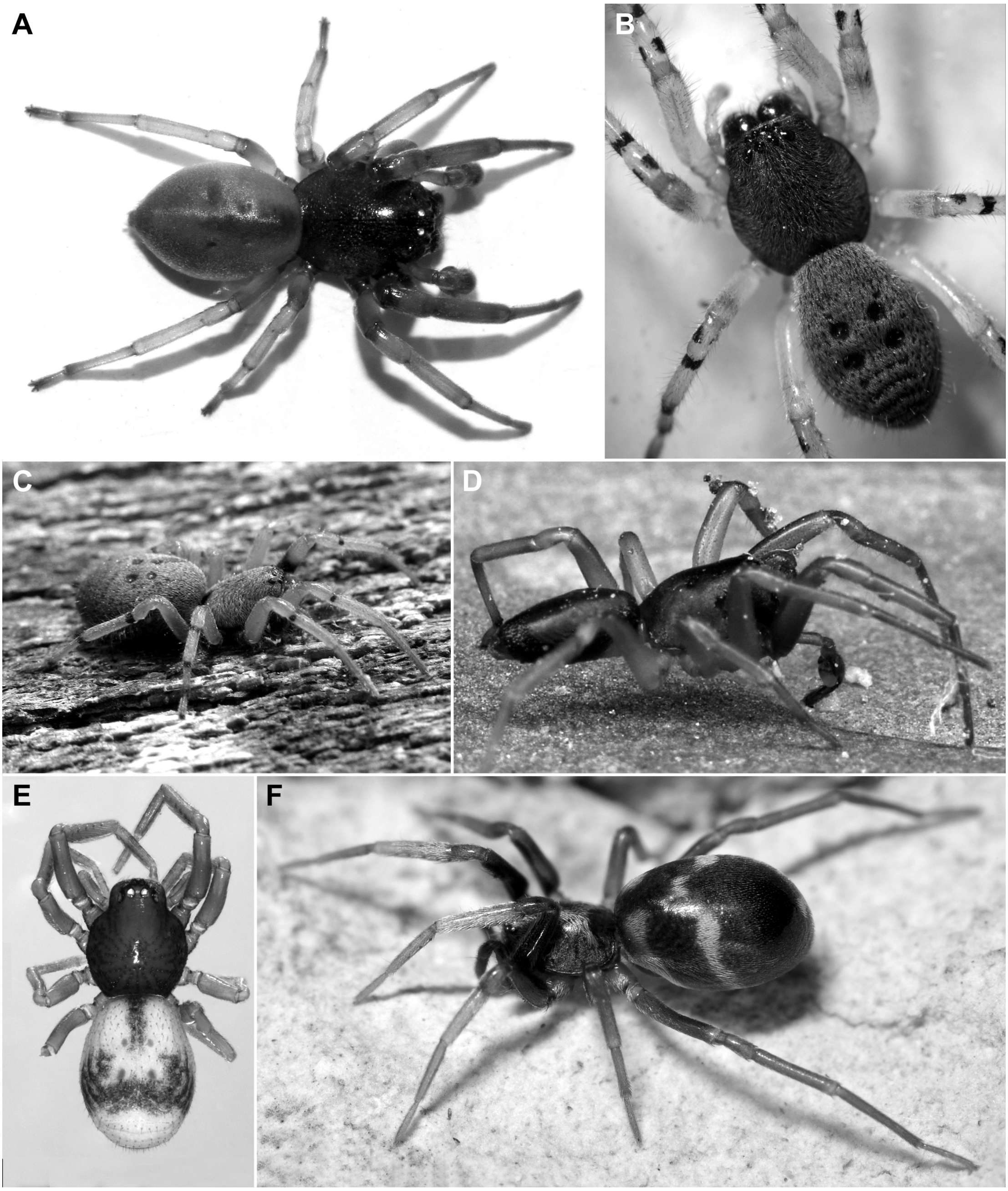


Fig. 226. Representatives of Trachelidae and Phrurolithidae. **A.** *Trachelas volutus* male (photo, Joseph T. Lapp). **B, C.** *Trachelopachys* sp. immature and female, respectively (photos, Ignacio Crudele). **D.** *Cetonana laticeps* male (photo, Jan Bosselaers). **E.** *Orthobula* sp. female (preserved, photo, Barbara Baehr). **F.** *Phrurolithus festivus* female (photo, Arno Grabolle).

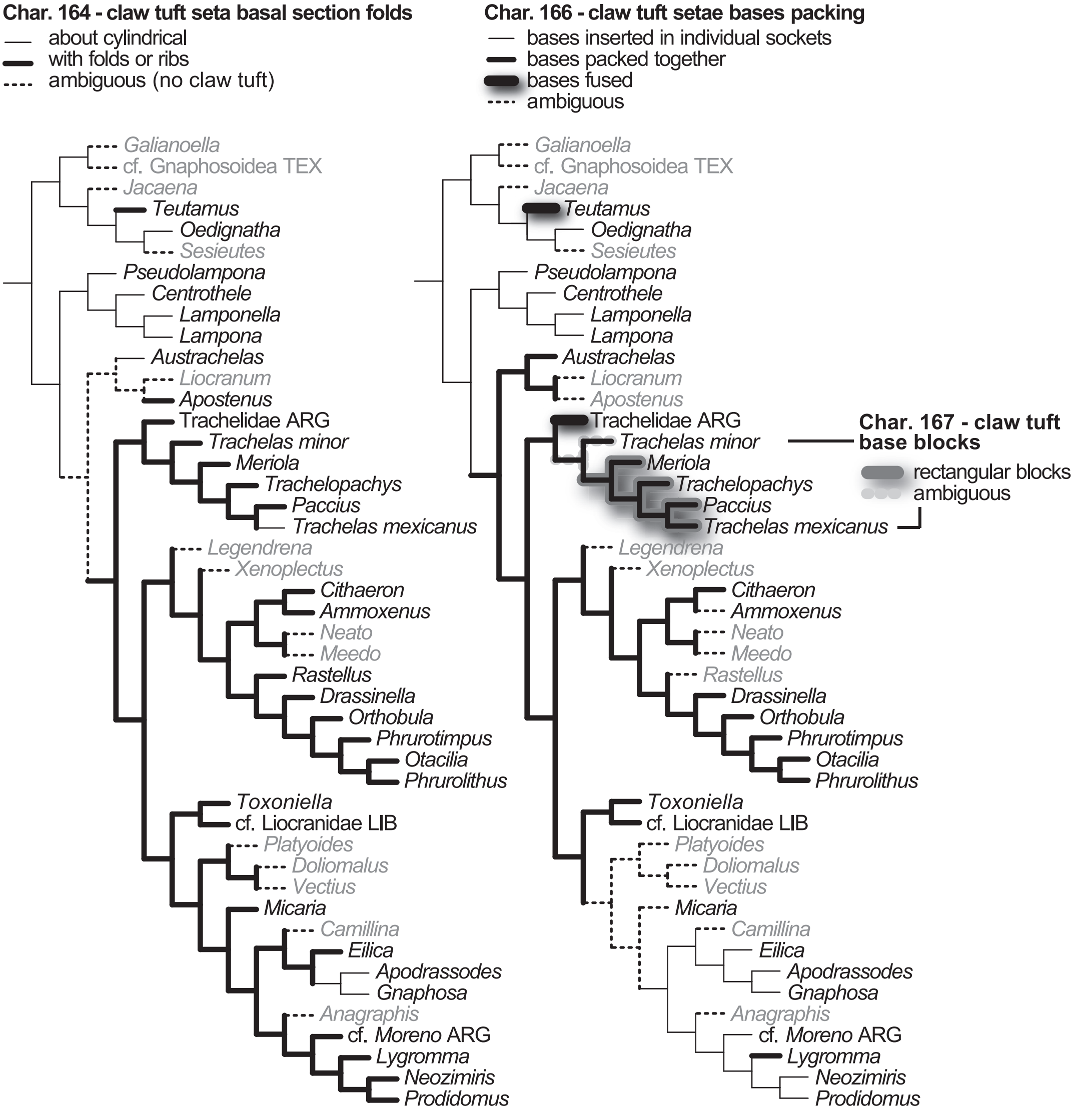

Char. 164 - claw tuft seta basal section folds
about cylindrical
with folds or ribs
ambiguous (no claw tuft)
Char. 166 - claw tuft setae bases packing
bases inserted in individual sockets
bases packed together
bases fused
ambiguous
Char. 167 - claw tuft base blocks
rectangular blocks
ambiguous
Galianoella
cf. Gnaphosoidea TEX
Jacaena
Teutamus
Oedignatha
Sesieutes
Pseudolampona
Centrothele
Lamponella
Lampona
Austrachelas
Liocranum
Apostenus
Trachelidae ARG
Trachelas minor
Meriola
Trachelopachys
Paccius
Trachelas mexicanus
Legendrena
Xenoplectus
Cithaeron
Ammoxenus
Neato
Meedo
Rastellus
Drassinella
Orthobula
Phrurotimpus
Otacilia
Phrurolithus
Toxoniella
cf. Liocranidae LIB
Platyoides
Doliomalus
Vectius
Micaria
Camillina
Eilica
Apodrassodes
Gnaphosa
Anagraphis
cf. Moreno ARG
Lygromma
Neozimiris
Prodidomus

Fig. 227. **A.** Mapping of the folding of claw tuft setae bases. **B.** Mapping of the packing or fusion of bases in common sockets and the block setal bases of Trachelidae.

later replaced the function of the claw hook with the claw lever (fig. 224A).

This analysis confirms Deeleman-Reinhold's (2001: 255) suggestion that the trachelines are unlikely members of Corinnidae. A constrained analysis forcing together the three classical subfamilies lacking a median apophysis (Corinninae, Castianeirinae, Trachelinae) is quite suboptimal, and does not show much improvement in fit in other characters (FD = 35.94, C/F = 1.75, table S16, see supplementary data: http://dx.doi.org/10.5531/sd.sp.4). Most of the character support placing trachelines far from Corinnidae comes from new characters presented here that concern the morphology of claw tufts and PME tapetum. A slightly different resolution, placing Trachelidae together with Phrurolithidae, as found by Bosselaers and Jocqué (2002), is less suboptimal, in large part because of the

TABLE 34
Synapomorphies of Phrurolithidae and internal clades
See figure 228A for clades, and table 11 for conventions.

RI	**Phrurolithidae, Clade 253**
0.09	fovea height relative to cephalon [2]: fovea as high or fovea lower → fovea highest
0.60	dorsal scutum on male abdomen [205]: absent → present
0.44	male epigastric sclerite [207]: absent → present
0.57	male palp femur ventral median apophysis [306]: absent → present
(0.48)	median apophysis [356]: present → absent
	Clade 250
0.29	cheliceral retromarginal teeth insertion [49]: distinct → on common base
0.38	major ampullates, number in female [253]: one, no nubbin → two
	Clade 251
0.35	abdomen anterior dorsal strong curved setae [213]: present → absent
1.00	endites sexual dimorphism [304]: not dimorphic → male basally globose
0.67	subtegulum transverse distally crossing piriform bulb [339]: other conformations → crossing (visible both sides)
0.44	subtegular locking lobe [341]: absent → present
0.44	tegular (embolar base) locking lobe [342]: absent → present
	Clade 252
0.17	palpal claw teeth [86]: one to several teeth → no teeth
0.42	spination legs III–IV dramatically reduced [144]: with spines → virtually no spines
0.34	female PMS aciniform spigots, number [276]: 4 or more, or 2–3 → 0
0.25	male PMS aciniform spigots, number [277]: 4 or more, or 2–3 → 1
0.26	receptacle in copulatory duct, in addition to primary and secondary spermathecae [374]: absent → between copulatory opening and primary spermatheca
1.00	globose membranous extension of proximal CD [375]: absent → present

eversion of Bennett's gland (char. 367), a character that is difficult to observe and, as a result, has a high proportion of missing entries; such a resolution, however, does not improve considerably the fit of other characters (C/F = 1.83; table S17 in supplementary data). At any rate, *Lessertina* is definitely placed in Eutichuridae, far from trachelines (fig. 204). Trachelidae ARG is superficially very similar to *Orthobula*, in size and appearance, but especially in the peculiar pore-bearing depressions on the carapace (char. 5) and the spinose forelegs. Forcing them together as sister groups is quite suboptimal, but such constrained analysis rescues some signal from other characters (FD = 22.86, C/F = 1.32), and places both genera among trachelids.

PHRUROLITHIDAE

The resolution obtained here for Phrurolithidae agrees with Penniman's (1985) proposal of a basal placement for *Drassinella*. Here the family (fig. 228, table 34) is joined by the ventral median process on the male palpal femur (char. 306), which may cooccur with a ventral apical process (char. 307), here ambiguously optimized at the base of the group. The rest of the synapomorphies come

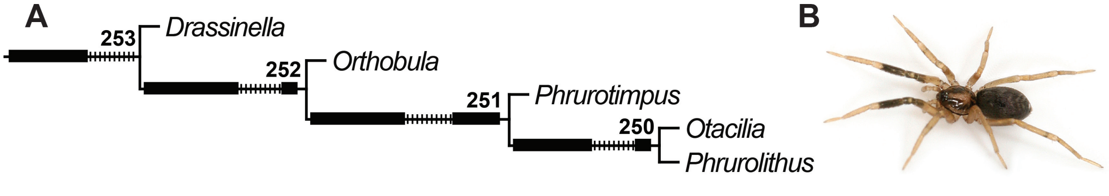


Fig. 228. **A.** Cladogram of Phrurolithidae. **B.** *Phrurotimpus borealis* female (photo, Tom Murray).

TABLE 35

Synapomorphies of groups related with Cithaeronidae, Ammoxenidae

See figure 220A for clades, and table 11 for conventions.

RI	***Cithaeron* + *Ammoxenus*, Clade 282**
0.17	female tarsi curvature [124]: straight, or slightly bent → strongly bent to coiled
0.89	ALS distal article at ectal margin [247]: external margin entire → external margin interrupted
	***Rastellus* + Phrurolithidae, Clade 254**
0.38	major ampullates, number in female [253]: two → one, no nubbin
0.42	major ampullates, number in male [258]: one, plus nubbin → one, no nubbin

from homoplasious characters, but the group is very uniform in somatic, spinneret, and genital morphology, especially in a group of higher phrurolithids (clade 251), for which the sexual dimorphism in endites (char. 304) is a promising character. All phrurolithids except *Drasinella* (clade 252) have a characteristic globose receptacle on the female internal genitalia (char. 374; Deeleman-Reinhold, 2001: 408); they also share a total absence of aciniform spigots on the female PMS (char. 276).

CITHAERONIDAE AND AMMOXENIDAE

Ammoxenidae is not monophyletic in this analysis (fig. 220A, table 35), except in one weighting scheme (for $k = 3$) and when some, but not all, ordered characters are treated as unordered (experiments 2 and 8; see table 3), where it appears as a sister group of *Cithaeron*, as obtained by Platnick (2002). A constrained analysis for Ammoxenidae results in a slightly suboptimal tree with almost as many characters performing better (C/F = 1.07; table S18, see supplementary material: http://dx.doi.org/10.5531/sd.sp.4). Two of the characters more strongly splitting apart the family are the curved, pseudosegmented tarsi (chars. 123, 124) not occurring in the more basal ammoxenids found in Australia; hence, a better sampling would probably recover the family as monophyletic. Unfortunately, those spiders are rare and could not be included in this study.

PRODIDOMIDAE

Platnick (1990) redefined the family Prodidomidae to include gnaphosoids with greatly elongated piriform gland spigot bases flanked by plumose setae. While the more basal cf. *Moreno* ARG has moderately elongated bases with loosely associated setae (char. 271, state 1; see also Platnick et al., 2005), the rest of the prodidomids have extremely elongated bases encircled by closely appressed setae (char. 271, state 2; see table 36).

The highly apomorphic Prodidominae (clade 269; fig. 230D) is the group with greatest support in the entire dataset (fig. 220). Among other characters, Prodidomines lack a serrula on the endite and on the cheliceral fang (chars. 74, 59), have extensive tracheal systems (chars. 220, 225, 226), and the spigots arise from flexible, annulate insertions (char. 238). There may be an additional synapomorphy in a distal tarsal pad made of two or three thick setae reported by Platnick and Penney (2004: fig. 15) for *Zimiris*, which are also found in *Prodidomus* and *Neozimiris* (fig. 82D, arrow). The polarized light detector of the PME is enhanced in *Prodidomus* to include the PLE as well (char. 28), which is probably a synapomorphy of the subfamily, perhaps together with Molycriinae (fig. 230C; see Platnick and Baehr, 2006: figs. 4–10).

Platnick and Baehr (2006) proposed the subfamily Theuminae for those prodidomids not included in Prodidominae or Molycriinae, here represented by *Lygromma* and cf. *Moreno* ARG. Such an arrangement is not supported in this analysis (table S19, see supplementary data: http://dx.doi.org/10.5531/sd.sp.4), especially because of the ALS spinning field of *Lygromma*, similar to those of prodidomines (and of molycriines as well). These authors clarified the placement of several gnaphosid genera sometimes included in Prodidomidae, of which one, *Anagraphis*, is included here. *Anagraphis* have ALS spinnerets intermediate between basal and higher gnaphosoids: the piriform gland spigots are large, but the shaft is not as widened as in typical Gnaphosidae, and there are

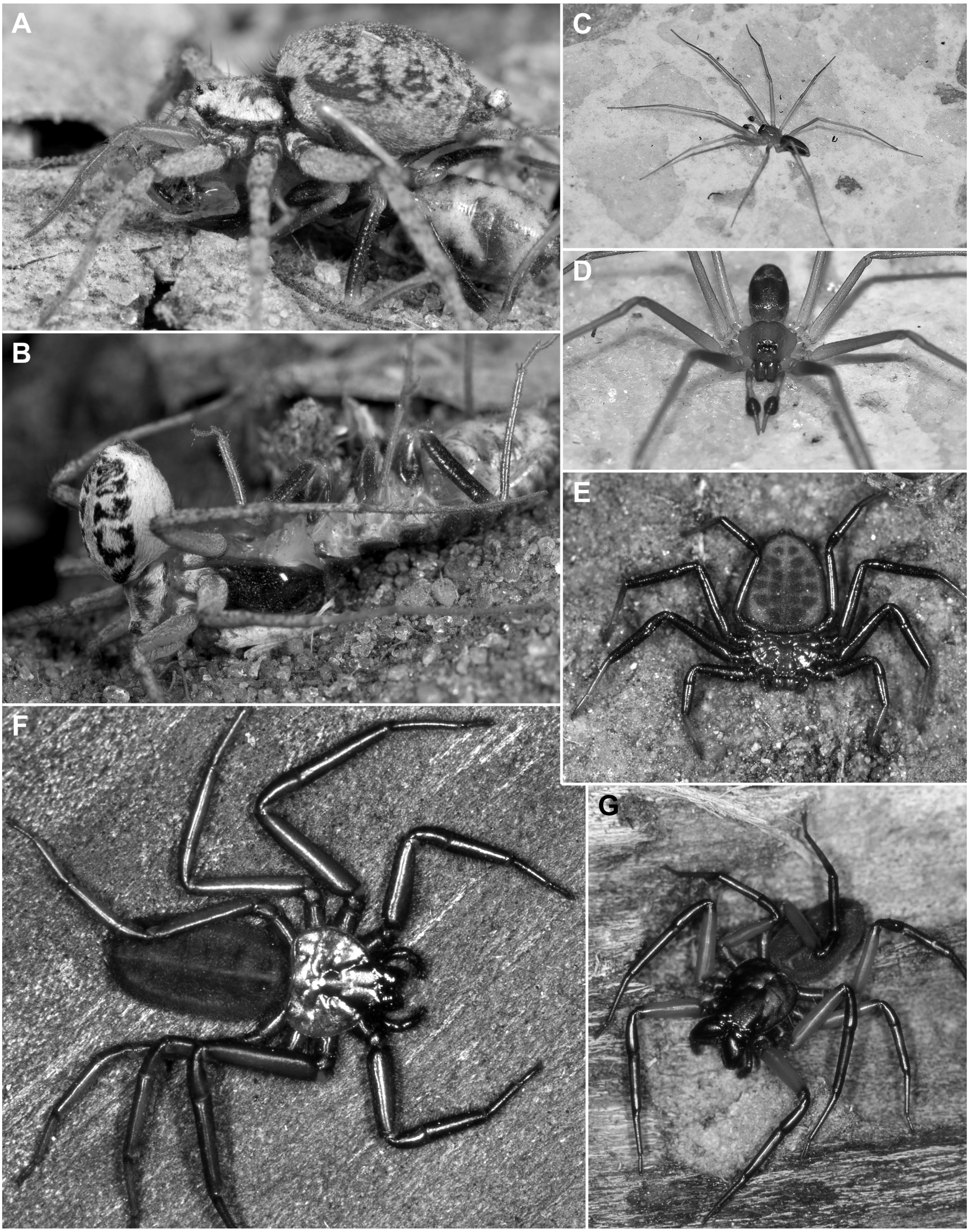


Fig. 229. Representatives of Ammoxenidae, Cithaeronidae and Trochanteriidae, habitus. **A, B.** *Ammoxenus* sp. female preying on a termite (photos, Piotr Naskrecki). **C, D.** *Cithaeron delimbatus* male (photos, John Koerner). **E.** *Vectius niger* immature. **F.** *Doliomalus cimicoides* female. **G.** *Platyoides walteri* female.

TABLE 36

Synapomorphies of Prodidomidae and internal clades

See figure 220A for clades, and table 11 for conventions.

RI	**Prodidomidae, Clade 271**
0.54	epiandrous spigots [214]: present → absent
0.50	female major ampullate shaft sizes [254]: both similar size → anterior much smaller than posterior
0.43	major ampullate field on anterior margin [256]: on mesal margin → on anterior margin
1.00	piriform spigots with elongate bases flanked by plumose setae [271]: base shorter than shaft → base longer, few setae
0.50	female PMS minor ampullates, number [273]: two → one no nubbin
0.36	male PMS minor ampullates, number [274]: one plus nubbin → one, no nubbin
0.53	PMS cylindrical gland spigots, number [283]: 4 → 3
0.55	cymbium dorsal chemosensory patch [324]: absent → present
	Clade 270
0.49	posterior eye row curvature [10]: approximately straight → notably procurved
0.17	scales axes, number [160]: one → two
0.67	tarsal scopula of tenent setae [161]: present → absent
1.00	major ampullate field projection [257]: major ampullate field on flat or slightly domed cuticle → major ampullate field on conical article
1.00	piriform spigots with elongate bases flanked by plumose setae [271]: base longer, few setae → base extreme length, encircling setae
	Prodidominae, Clade 269
0.45	thoracic fovea [0]: present → absent
0.41	cheliceral boss [38]: present → absent
0.25	fang shaft serrula [59]: present → absent
0.14	serrula [74]: present → absent
0.53	female palpal tarsus dorsal chemosensory setae distribution [83]: scattered → in a defined patch
0.29	palpal claw [85]: present → reduced to nubbin
0.50	sternum shape [89]: shield shaped → oval
0.67	retrocoxal hymen [102]: leg I → absent
0.33	trochanter IV length [106]: less than 1.5 times length of trochanter III → 1.5 times as long as trochanter III or longer
0.47	spination legs I–II dramatically reduced [143]: with spines → virtually no spines
0.60	claw–claw tuft clasping mechanism structure [170]: teeth appressed together → solid
0.71	claw tuft insertion [173]: continuous with lateral cuticle → delimited plate separated by soft area from lateral cuticle
0.62	lateral tracheae branching [220]: simple, linear → branched
0.59	median tracheae branching [225]: unbranched → strongly branched
0.62	median tracheae passing to carapace [226]: limited to abdomen → two large trunks with many ramifications passing to carapace
1.00	spigots insertion articulation [238]: continuous or simple fold → annulate flexible
0.50	ALS separation [243]: separate about a diameter or more → contiguous
0.50	PMS-PLS anterior claviform setae [292]: absent → present
1.00	PLS rows of claviform setae [293]: absent → present

remnants of a terminal article (fig. 128F; Platnick and Baehr, 2006). Constraining *Anagraphis* together with Gnaphosidae (but without *Micaria*; table S20 in supplementary material) produces a slightly suboptimal tree with *Anagraphis* in a basal position.

GNAPHOSIDAE

This analysis recovered a more narrowly defined Gnaphosidae (fig. 220A, table 37), supported by the widened piriform gland spigot shaft, with a shaft-base transition continuous in curvature, only with a superficial marking. The disputed members of the family that have been included here (*Micaria*, *Anagraphis*, *Vectius*) all have a well-defined constriction marking the shaft-base transition. When those three terminals were constrained to be members of Gnaphosidae, they consistently appeared as sister to all other gnaphosids, without any sensible synapomorphy for the family (fig. 231A–C; tables S21–S23, see supplementary material: http://dx.doi.org/10.5531/sd.sp.4). The inclusion of further representatives might of course challenge these results

TABLE 37
Synapomorphies of Gnaphosidae and internal clades
See figure 220A for clades, and table 11 for conventions.

RI	
	Gnaphosidae, Clade 268
1.00	piriform shaft-base transition [263]: well-defined change in curvature → continuous curvature only superficial marking
0.24	conductor [359]: present → absent
	Clade 266
0.82	claw tuft seta basal section folds [164]: with folds or ribs → nearly cylindrical
0.94	claw tuft seta base thickness [165]: thick base → thin base
0.53	PMS cylindrical gland spigots, number [283]: 4 → many
	Clade 267
0.66	precoxal triangles in female [95]: fused to sternum → separate from sternum

(e.g., the extremely flat *Hemicloea*, and members of Drassodinae, with a constriction on the pirigorm gland spigots; see Platnick, 1990: figs. 68, 80, 147; Murphy, 2007: 583).

TAXONOMY

Recent workers have found that three of the dionychan families, Miturgidae, Corinnidae, and Liocranidae, are not operational as currently defined (Deeleman-Reinhold, 2001; Bosselaers and Jocqué, 2002; Raven, 2009; Versteirt et al., 2010; Bonaldo et al., 2012). Because several of the high-level groups from this analysis are weakly supported, the taxonomic changes here proposed are limited to a few clear-cut cases that can be solved with the current selection of representatives.

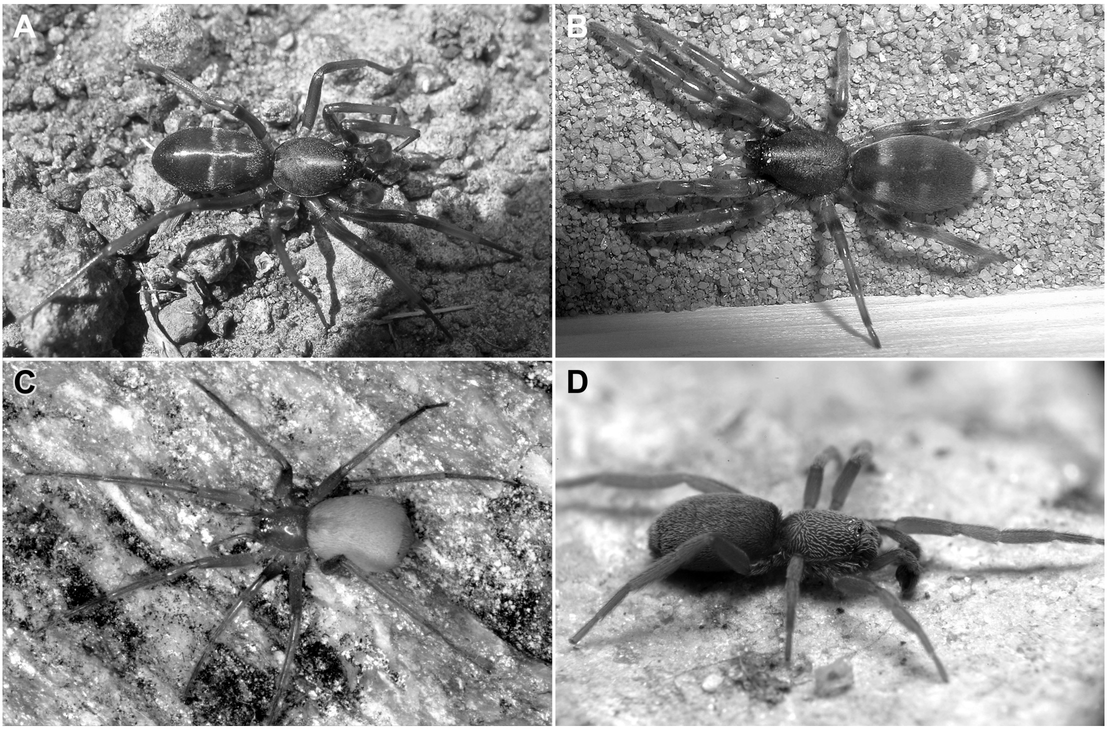


Fig. 230. Representatives of Lamponidae and Prodidomidae, habitus. **A.** *Centrothele* sp. penultimate male (photo, Robert Raven). **B.** *Lampona murina* female (photo, Robert Raven). **C.** *Zimiris doriai* female (photo, Peter Jäger). **D.** *Prodidomus amaranthinus* male (photo, Rudolph Macek).

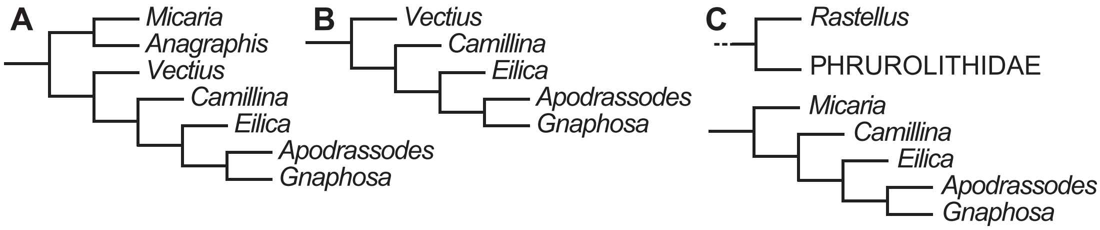


Fig. 231. Alternative resolutions of Gnaphosidae using constrained searches. **A.** Gnaphosidae with *Micaria*, *Vectius* and *Anagraphis* (no synapomorphies, FD = 52.19, C/F = 4.21; see table S21). **B.** Gnaphosidae with *Vectius* (synapomorphies: char. 154, scales absent; char. 376, cuticular glands on epigyne present; FD = 44.71, C/F = 2.00; see table S22). **C.** Gnaphosidae with *Micaria* (no synapomorphies, FD = 7.34, no character increases its fit; see table S23).

Families are especially important for the organization of collections, catalogs, chapters, inventories, and even concepts as ecological guilds, where taxonomic changes affect the work of many biological disciplines in a very concrete way. In contrast, higher-level groups, such as superfamilies or clades of closely related families, usually have a more academic interest. Three subfamilies that have been switching positions from family to family in recent years (Eutichurinae, Phrurolithinae, Trachelinae) are sufficiently homogeneous and diverse to be considered families of their own. In this way, the need for a stable familial classification can be fullfilled, separately from the ongoing research on relationships among higher groups.

After the few taxonomic changes introduced below, the systematics of the dionychan spiders can be summarized as follows: The monophyly of most dionychan families appear as reasonably established (namely, Sparassidae, Selenopidae, Salticidae, Philodromidae, Thomisidae, Trachelidae, Phrurolithidae, Lamponidae, and Prodidomidae). Some families have a well-defined core group, but also include some problematic members or clades (Anyphaenidae, Clubionidae, Eutichuridae, and Miturgidae) that are retained for want of a better placement. A few other families (Trochanteriidae, Gallieniellidae, Ammoxenidae, and Gnaphosidae) were not recovered as monophyletic, and may need a better taxon sampling for adequate resolution, while it was not possible to test the monophyly of Cithaeronidae. Liocranidae and Corinnidae are decidedly not monophyletic, perhaps the most difficult taxonomic problems highlighted in this study.

EUTICHURIDAE LEHTINEN, NEW RANK

Eutichurinae Lehtinen, 1967. Type genus: *Eutichurus* Simon, 1896.

While the monophyly of Eutichurinae is reasonably uncontroversial, the ongoing discussion is focused on its placement in either Clubionidae or Miturgidae (see Ramírez et al., 1997; Deeleman-Reinhold, 2001; Raven, 2009; Bonaldo et al., 2012). This analysis provides some guide as to the relationships of the groups involved, but everything indicates that the hypotheses of higher-level relationships will continue to fluctuate for a while.

DIAGNOSIS: Eutichurids have an RTA, two claws, and claw tuft. They differ from other dionychans by having the anterior lateral spinnerets conical and contiguous, not sexually dimorphic, posterior median spinnerets conical, cylindrical gland spigots small, similar to aciniforms or absent, posterior lateral spinnerets with distal article usually elongate, eye group wide, spanning the entire width of the caput, lateral eyes placed together on raised tubercles, usually without thoracic fovea, without thick, curved setae on the anterior dorsal abdomen. The tapetum of the indirect eyes has a median band of dark holes, instead of a definite dark line. Some species of *Cheiracanthium* may have a shallow thoracic fovea and a canoe tapetum, but have a posteriorly extending retrolateral margin of the cymbium as in several other eutichurids.

NOTE: *Strotarchus* is provisionally placed here (see Main Clades of Dionycha: Eutichuridae and Bonaldo et al., 2012).

Wagner (1887) created the family "Cheiracantidae" after *Cheiracanthium* C.L. Koch. His original spelling has to be corrected as Cheiracanthidae (after the correct original spelling *Cheiracanthium*; ICZN: 32.5.3.3). Soon thereafter, Simon (1897) placed *Cheiracanthium* in Clubionidae near *Clubiona*, in his group Clubioneae, without any mention to Wagner (1887), thus the family name "Cheiracanthidae" was unused for more than a century. The placement of *Cheiracanthium* in Clubionidae remained stable until Ramírez et al. (1997) argued that the genus was related instead to *Eutichurus*, *Macerio*, and other genera that were grouped in the subfamily Eutichurinae, created by Lehtinen (1967) under Miturgidae (see Bonaldo, 1994). It passed unnoticed that the transfer of *Cheiracanthium* to Eutichurinae implies the synonymy of Eutichurinae with the older, but forgotten name Cheiracanthidae.

It turns out that Cheiracanth-, a combination of the Greek words "hand" and "spine" has been used as a stem for other animal genera as well, including two family-rank names: Cheiracanthidae, a family created by Berg (1940) for fossil acanthodiform fishes after *Cheiracanthus* Agassiz, and Cheiracanthidea Diesling, 1861, after the nematode *Cheiracanthus* Diesing, now a junior synonym of *Gnathostoma* Owen, thus a synonym of Gnathostomatidae (Baylis and Daubney, 1926), but still available. The name Eutichuridae, after Lehtinen's Eutichurinae is an available replacement for the spider name Cheiracanthidae. The spider family name Cheiracanthidae should have been formed with a double "i" ("Cheiracanthiidae"), similar to Mecicobothriidae after *Mecicobothrium* and Theridiidae after *Theridion* (Marusik and Kovblyuk, 2011). That spelling would avoid the two homonyms, but the Code does not list such a possibility as a justified emendation (ICZN: 32.5.3, 33.2.3); the same is true for the spelling "Chiracanthiidae" used by Ono (2009), because "*Chiracanthium*" is an unjustified emendation of *Cheiracanthium* (see Platnick, 2012, and Bonnet, 1956: 1047). In any case, none of the alternative spellings that would avoid homonymy qualify as emendations of prevailing use (ICZN 33.2.3.1).

Genera included: *Calamoneta*, *Calamopus*, *Cheiracanthium*, *Cheiramiona*, *Ericaella*, *Eutichurus*, *Macerio*, *Radulphius*, *Summacanthium*, *Tecution* (all transferred from Miturgidae), and *Lessertina* (transferred from Corinnidae). Provisionally placed here: *Strotarchus* (transferred from Miturgidae).

MITURGIDAE

Miturgini Simon, 1886: 373. Type genus: *Miturga* Thorell, 1870.

Zorinae O. P.-Cambridge, 1893: 132. Type genus: *Zora* C.L. Koch, 1847. New synonymy.

The recent phylogenetic analyses obtained zorids and miturgids as a monophyletic group with a rather uniform somatic morphology, and here *Zora* appears well nested within the classical miturgines. The two families are currently distinguished by subtleties of the male genitalia (Raven and Stumkat, 2003). On the light of this evidence, it seems adequate to reunite all these very similar genera of miturgines and zorids under the single family name Miturgidae. Even if they turned out to be monophyletic sister groups, they could still be distinguished as subfamilies. The *Xenoctenus* group, currently placed in Zoridae, probably deserves family status as well. Until this is clarified, listing the group under Miturgidae until its relationships are better known seems equally efficient as the previous placement among zorids.

DIAGNOSIS: Miturgids have RTA and two claws. Most miturgids differ from other dionychans or lycosoids by having an RTA with a canal and a membranous area, and a retrolateral groove on the cymbium. The embolus arises centrally on the tegulum, with the median apophysis arising in a continuum from its base, directed forward.

Genera included: *Diaprograpta*, *Eupograpta*, *Mituliodon*, *Miturga*, *Mitzoruga*, *Nuliodon*, *Prochora*, *Syrisca*, *Syspira*, *Teminius*, *Zealoctenus*. The following genera were listed in Zoridae, and are here transferred to Miturgidae, mostly following Raven and Stumkat (2003): *Argoctenus*, *Elassoctenus*, *Hestimodema*, *Odomasta*, *Simonus*, *Thasyraea*, *Tuxoctenus*, and *Zora*. The following genera, currently listed in Systariinae are provisionally kept in Miturgidae, according to the results obtained here: *Palicanus*, *Systaria*, *Tamin*, *Xantharia*. The following genera currently listed in Zoridae and Ctenidae belong to the *Xenoctenus* group, and are provisionally listed in Miturgidae until their family status is clarified: *Odo*, *Paravulsor* (transferred from Ctenidae) and *Xenoctenus*. The following genera are provisionally listed in Miturgidae until their relationships are better established: *Pacificana, Parapostenus, Hoedillus* (perhaps *Xenoctenus* group), *Israzorides* (perhaps a Zoropsidae, similar to *Pseudoctenus thaleri*), *Pseudoceto* (transferred from Corinnidae; a miturgine, according to A. Brescovit in Bonaldo, 2000: 34), *Voraptus*, and *Zoroides* (most probably a Phrurolithidae, see also Silva Davila, 2003).

The following genera are transferred to Eutichuridae (see above): *Calamoneta*, *Calamopus*, *Cheiracanthium*, *Cheiramiona*, *Ericaella*, *Eutichurus*, *Macerio*, *Radulphius*, *Strotarchus*, *Summacanthium*, and *Tecution*.

TRACHELIDAE SIMON, NEW RANK

Tracheleae Simon, 1897: 178. Type genus: *Trachelas* L. Koch, 1872.

This analysis is conclusive in the relationships of trachelines in the CTC clade, together with phrurolithines and gnaphosoids, far from its current placement in Corinnidae. This is in agreement with the ideas anticipated by Deeleman-Reinhold (2001: 255), and at this point it is clear that raising the trachelines to family level will provide a good service to spider taxonomy. Lehtinen (1996: 409) has already referred to the group as Trachelidae, but without any comment of justification; hence, it is unclear whether he really meant to propose it as a new family group, or he just committed a lapsus. Platnick and Ewing (1995) noted that the absence of leg spines and the male cusples were not universal in trachelines, and Haddad (2006) described *Spinotrachelas capensis*, a tracheline genus with many spines on their anterior tibiae, plus cusples on the metatarsus, and later (Haddad and Lyle, 2008) described *Poachelas*, including species with heavily spinose forelegs, that could be absent in females of some species. They reasonably suggested that *Spinotrachelas* and *Poachelas*, by their abundant spines, could be basal trachelines. The enigmatic Trachelidae ARG included here also has a long series of ventral macrosetae on the two anterior pairs of legs, and is accordingly placed as a basal member of the family. The reduction of leg spines is in fact a frequent syndrome in the OMT clade (fig. 192C), but also in several Eutichuridae and Thomisidae, to name just a few.

DIAGNOSIS: Most trachelids are similar to phrurolithids in having claw tufts made of heavily folded setae, a claw tuft clasper, and reduced leg spination especially on posterior legs and dorsally on all femora, and lacking a median apophysis on the male copulatory bulb, but can be distinguished by lacking the ventral distal hook on the male palpal femur. At least several of the trachelid genera have uniquely shaped bases of the claw tuft setae, in the form of rectangular blocks. With a few exceptions, most of the trachelid species lack macrosetae altogether, and the males have leg cusples.

Genera included: *Afroceto*, *Cetonana*, *Fuchiba*, *Fuchibotulus*, *Meriola*, *Metatrachelas*, *Paccius*, *Paratrachelas*, *Patelloceto*, *Planochelas*, *Poachelas*, *Spinotrachelas*, *Thysanina*, *Trachelas*, *Trachelopachys*, and *Utivarachna*.

PHRUROLITHIDAE BANKS, NEW RANK

Phrurolithi Banks, 1892: 94. Type genus: *Phrurolithus* C.L. Koch, 1839.

Similar to the case with trachelids, this analysis clearly places phrurolithines in the CTC clade, far from its current placement in Corinnidae; note that Lehtinen (1967: 259, 291, 415) argued in favor of the placement of phrurolithines in Gnaphosidae. Again, raising the phrurolithines to family status is in agreement with the ideas anticipated by Deeleman-Reinhold (2001), and will help in providing a more stable and intuitive classification at the family level.

DIAGNOSIS: Phrurolithids are similar to trachelids in having claw tufts made of heavily folded setae, a claw tuft clasper and reduced leg spination especially on posterior legs and dorsally on all femora, and lacking a median apophysis on the male copulatory bulb, but can be distinguished by having modifications on the ventral side of the male palpal femur, especially a ventral median apophysis and usually a ventral apical hook. All phrurolithids except *Drasinella* have a characteristic globose receptacle on the female internal genitalia, in addition to the primary and secondary spermathecae. Phrurolithids differ from most trachelids by having a long series of ventral macrosetae on the anterior tibiae, and by lacking cusples.

Genera included: *Abdosetae*, *Dorymetaecus* (transferred from Clubionidae), *Drassinella*, *Liophrurillus*, *Orthobula*, *Otacilia*, *Phonotimpus*, *Phrurolinillus*, *Phrurolithus*, *Phruronellus*, *Phrurotimpus*, *Piabuna*, *Plynnon*, and *Scotinella*.

Dorymetaecus Rainbow, 1920: 259. Type species *D. spinnipes* Rainbow, 1920. The female holotype is discolored and damaged, and has several larger body parts (a leg tarsus, one ALS, and one PLS, probably of a gnaphosid) that evidently come from other specimens in the same vial. The female genitalia are similar to that of *Otacilia sinifera* Deeleman-Reinhold (2001: fig. 669), including the large, globose receptacles. The anterior legs with multiple series of long spines (Rainbow, 1920: fig. 85) and the narrow cephalic area suggest that this species may belong in *Otacilia*.

LIOCRANIDAE

Liocraninae Simon, 1897: 124. Type genus: *Liocranum* L. Koch, 1866.

In this analysis the genus *Liocranum* is well nested within the OMT clade. Of the potential relatives included in this dataset (phrurolithids, *Toxoniella*, *Xenoplectus*, cf. Liocranidae LIB, *Agroeca*, *Neoanagraphis*, *Donuea*, *Jacaena*, *Sesieutes*, *Teutamus*, *Hortipes*, *Apostenus*, *Austrachelas*), only the last two turned out to be closely associated with *Liocranum*. Deeleman-Reinhold (2001: 407) listed the heavily sclerotized genera *Sesieutes*, *Jacaena*, *Teutamus*, and *Sphingius* in Phrurolithinae, and noted that the characteristics of the subfamily (depressed endites, oval posterior median eyes, enlarged and laterally compressed female posterior median spinnerets) were also found in Gnaphosidae. These are common characters in the larger OMT clade as proposed here, including phrurolithids and gnaphosoids. Here the three genera *Sesieutes*, *Jacaena*, and *Teutamus* appear together in a well-defined clade, the *Teutamus* group, with further synapomorphies: the teeth of the superior tarsal claws inserted on a mesal line, two rows of trichobothria on the male palpal cymbium, and a heavily sclerotized body, including an epigastric sclerite in both sexes, that of the male surrounding the pedicel base, and no lateral tracheae. These are characters also found in other members of the OMT clade, and *Oedignatha* diverges significantly from this group. The *Teutamus* group may deserve familial status, but the inclusion of *Oedignatha* is not convincing and carries a nomenclatural burden. A family-level name is available after Oedignathae by Simon (1897: 187), but the genus diverges widely from the rest of the group (e.g., it lacks the orthogonal PME tapetum and the depressed endites of the OMT clade, among many other characters; see table 30). This situation should be more adequately solved with an analysis including *Sphingius*, and especially *Koppe*, which is very close to *Oedignatha* Deeleman-Reinhold (2001: 257). For the time being, it seems convenient to leave the *Teutamus* group in Liocranidae, where they are currently, which at least places them in the OMT clade, and transferring *Oedignatha* and *Koppe* to Liocranidae. I think it is not advisable at this point to commit further nomenclatural changes in the remaining genera not clearly associated with any of the currently established families. In its present composition, the family is clearly not monophyletic, but still the majority of its members have the characteristic tapetum disposition of the OMT Clade.

Genera included in the *Teutamus* group: *Jacaena*, *Sesieutes*, *Sphingius*, *Teutamus*, and probably also *Sudharmia*, *Oedignatha*, and *Koppe* (the last two transferred from Corinnidae).

Other genera included in Liocranidae: *Agraecina*, *Agroeca*, *Andromma*, *Apostenus*, *Arabelia*, *Argistes*, *Coryssiphus*, *Cteniogaster*, *Cybaeodes*, *Donuea*, *Hesperocranum*, *Heterochemmis*, *Laudetia*, *Liocranoeca*, *Liocranum*, *Liparochrysis*, *Mesiothelus*, *Mesobria*, *Neoanagraphis*, *Paratus*, *Rhaeboctesis*, *Sagana*, *Scotina*, *Toxoniella*, and *Vankeeria*.

CORINNIDAE

The heterogeneity of Corinnidae is here alleviated by the exclusion of trachelids and phrurolithids. Of the genera still remaining in the family, most are listed in the subfamilies Corinninae or Castianeirinae, which are reasonably defined, most probably monophyletic, and sister groups (see above). Of the remaining genera with uncertain relationships, several are here loosely grouped in the *Pronophaea* group (*Brachyphaea*, *Mandaneta*, *Olbus*, *Procopius*, *Pronophaea*, *Pseudocorinna*, and probably also *Austrophaea*, *Crinopseudoa*, *Ianduba*, and *Vendaphaea*), one is perhaps related with eutichurids or anyphaenids (*Hortipes*), and the rest are very poorly known (*Arushina*, *Cycais*, and *Scorteccia*). In its current composition, the family is certainly not monophyletic, but at least its members lack the characteristic tapetum and claws of the better-defined OMT and CTC Clades.

Genera included in Corinninae: *Abapeba*, *Attacobius*, *Corinna*, *Creugas*, *Ecitocobius*, *Erendira*, *Falconina*, *Megalostrata*, *Methesis*, *Parachemmis*, *Paradiestus*, *Septentrinna*, *Simonestus*, *Stethorrhagus*, *Tapixaua*, *Tupirinna*, and *Xeropigo*.

Genera included in Castianeirinae: *Aetius*, *Apochinomma*, *Cambalida*, *Castanilla*, *Castianeira*, *Castoponera*, *Coenoptychus*, *Copa*, *Corinnomma*, *Echinax*, *Graptartia*, *Humua*, *Mazax*, *Medmassa*, *Merenius*, *Messapus*, *Myrmecium*, *Myrmecotypus*, *Poecilipta*, *Pranburia*, *Psellocoptus*, *Serendib*, *Sphecotypus*, and *Supunna*.

CLUBIONIDAE

After the reconfiguration of Clubionidae made by Lehtinen (1967) and the increased attention to silk gland spigots in spider taxonomy (Platnick, 1990), our concept of Clubionidae started to converge in a restricted and most probably monophyletic group, the Clubioninae. The remaining genera (*Carteroniella*, *Carteronius*, *Clubionina*, and *Tixcocoba*) are all poorly known.

Genera included in Clubioninae: *Arabellata*, *Clubiona*, *Elaver*, *Invexillata*, *Malamatidia*, *Matidia*, *Nusatidia*, *Pristidia*, *Pteroneta*, *Scopalio*, and *Simalio*.

TENGELLIDAE

Tengellidae Dahl, 1908: 194. Type genus: *Tengella* Dahl, 1901.

The genus *Ciniflella* was described by Mello-Leitão in Dictynidae, and transferred by Lehtinen to "Amaurobiidae: Metaltellinae." I have included two species from Brazil and Argentina, identified by comparison with drawings of *C. lutea* (Mello-Leitão), the type species of the genus (thanks to Lina Almeida). *Ciniflella* species have an oval calamistrum (fig. 52B), and also a file of regularly disposed ridges on the male RTA (fig. 143C) similar to that in the Australian "tengellid" *Austrotengella* recently described by Raven (2012). The male and female genitalia are also similar (figs. 143B, 171B, C), although the Australian species are ecribellate. Following the strategy of Raven, and in absence of a better familial placement, *Ciniflella* is here transferred to Tengellidae.

Genera included in Tengellidae: *Anachemmis*, *Austrotengella*, *Calamistrula*, *Ciniflella*, *Lauricius*, *Liocranoides*, *Socalchemmis*, *Tengella*, *Titiotus*, and *Wiltona*.

ACKNOWLEDGMENTS

This work was made possible by the generous support of Norman Platnick, who consistently encouraged my work and offered decisive guidance since my early beginnings in arachnology. Platnick provided the most stimulating environment during my postdoctoral stay at AMNH, allowing me a total freedom of criteria, even though he may not share some of the conclusions presented here. The participants of the AToL Spiders project, especially Ward Wheeler, provided support for completion of the work presented here, including an extensive exploration and criticism of legacy characters. Charles Griswold, Norman Platnick, Cristian Grismado, Luis Piacentini, and Juan Manuel Andía Navarro provided valuable comments on versions of this manuscript. Robert Raven, and especially Mary Knight from Scientific Publications, AMNH, are thanked by the meticulous correction and useful linguistic suggestions for this manuscript; the mistakes that may remain are my responsibility. This work benefited from discussions on systematics and morphology with the following colleagues: Alexandre Bonaldo (Miturgidae, Eutichuridae, Corinnidae), Jan Bosselaers (dionychans, Zoropsidae), Rudy Jocqué (Corinnidae, Liocranidae, Zodariidae), Norman Platnick (all taxa), Charles Griswold (outgroups and anatomy), Marshal Hedin (*Homalonychus*), Bernhard Huber, Fernando Álvarez Padilla (genitalia), Elke Jenschel, Arno Lise, and Suresh Benjamin (Thomisidae), Gustavo Hormiga (outgroups), Jonathan Coddington (outgroups, behavior), Cristina Scioscia, Wayne Maddison, and G.B. Edwards (Salticidae), Mark Townley (anatomy of spinnerets), Darrell Ubick (Liocranidae), Robert Raven (Miturgidae, Corinnidae), Luis Piacentini (lycosid genitalia), Tharina Bird (Ammoxenidae), Lucrecia Nieto (Filistatidae), José Corronca (Selenopidae), Fernando Costa (Zodariidae), Charles Haddad and David Candiani (Corinnidae), Vladimir Ovtsharenko (Gnaphosidae), Matías Izquierdo (Orsolobidae), Antonio Brescovit (Ctenidae), Kefyn Catley (Hypochilidae), Roberto Keller, Ward Wheeler, and Toby Schuh (systematics). Junxia Zhang helped coordinate the phylogenetic characters here presented with the Spiders AToL project. I thank the following institutions and curators for providing the specimens on which this study is based: American Museum of Natural History, New York (AMNH, Norman Platnick); Australian Museum, Sydney (AMS, M. Gray); California Academy of Sciences, San Francisco (CAS, Charles Griswold); Central Victoria Regional Insect Collection, La Trobe University, Bendigo, Victoria (CVIC, J. Shield); Florida State Collection of Arthropods, Gainesville (FSCA, G.B. Edwards); Instituto Butantan, São Paulo (IBSP, Antonio Brescovit); Institute of Ecology and Biological Resources, Hanoi, Vietnam (IEBR); Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (INBIO, Carlos Viquez); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSN, Léon Baert); Collection of Arachnids, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, (MACN-Ar, Cristina Scioscia); Muséum National d'Histoire Naturelle, Paris (MHNP, Christine Rollard); Koninklijk Museum voor Midden-Afrika, Tervuren (MRAC, Rudy Jocqué); Museo de Historia Natural, Universidad Mayor de San Marcos (MUSM, Diana Silva Dávila); National Collection of Arachnida, Plant Protection Research Institute, Pretoria (NCA, Ansie Dippenaar-Schoeman); National Museum (Natural History) of Zimbabwe, Bulawayo (NMZ); Otago Museum, Dunedin (OMD, J. Darby); Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul (PUC, Arno Lise); Queensland Museum, Brisbane (QMB, QM, QMS, R. Raven); San Diego State University (SDSU, Marshal Hedin); University of British Columbia, Beaty Biodiversity Museum (UBC, Wayne Maddison); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM, Jonathan Coddington); Western Australian Museum, Perth (WAM, M. Harvey, J. Waldock); Zoologisk Museum, Copenhagen (ZMUC, Nikolaj Scharff). The following persons are also acknowledged for providing access to further specimens: Alessio Trotta, Alexandre Bonaldo, Barbara Baehr, Charles Haddad, Cristian Grismado, Darrel Ubick, David Richman, Fred Coyle, Gonzalo Rubio, Gustavo Hormiga, Ingi Agnarsson, Jason Bond, Jean Kekenbosch, Jeremy Miller, Lara Lopardo, Lisa Boutin, Lorenzo Prendini, Mark Townley, Matjaz Kuntner, Nicolás López, Pablo Goloboff, Rick Vetter, Suresh Benjamin, Tharina Bird, and Vladimir Ovtsharenko. I am indebted to the colleagues that identified specimens from images: Sarah Crews, Charles Haddad, Robert Raven, and Tharina Bird. Dave Grimaldi and Roy Larimer gave access and help for digital imaging. Bernhard Huber, Diana Silva Dávila, Fernando Álvarez Padilla, and Gustavo Hormiga provided advice and inspiration for preparation of samples. Angela Klaus and Kevin Frischmann provided extensive help with the SEM imaging, preparation of specimens and imaging software at AMNH.

Fabián Tricárico provided continuous support at the SEM facility in MACN. Darrell Ubick, Vladimir Ovtsharenko, Norman Platnick, Alexandre Bonaldo, Diana Silva Dávila, Charles Haddad, Nikolaj Scharff, Lara Lopardo, Renner Baptista, and Abel Pérez González provided additional images used for the phylogenetic analysis. Cristian Grismado, Paola Favre, Facundo Labarque, Matías Izquierdo, and Junxia Zhang produced several of the images in the Buenos Aires lab. Greg Riccardi and Deb Paul provided immense support in processing the image collection in Morphbank. I am indebted to the following persons for providing the exceptional images of living specimens, including the first published photographs for many: Alan Cressler, Aloysius Staudt, Arno Grabolle, Arthur Anker, Barbara Baehr, Charles Haddad, Cristian Grismado, David Richman, Gonzalo Rubio, Guido Gabriel, Hans Henderickx, Ignacio Crudele, Jan Bosselaers, Jillian Cowles, John Koerner, John Koerner (www.johnkoerner.org), Joseph T. Lapp (http://spiderjoe.com/), Marshall Hedin, Paul Bertner, Peter Jäger, Piotr Naskrecki, Robert Raven, Roger S. Key, Rudolph Macek, Rudy Jocqué, Seig Kopinitz, Sidclay Dias, Stefan Sollfors, Tom Murray, and Yixiong Cai. Fieldwork was made possible thanks to the following institutions, which also provided extensive support in the field: Administración de Parques Nacionales (Argentina), Corporación Nacional Forestal (CONAF, Chile), KwaZulu-Natal Nature Conservation Service (South Africa), Instituto Nacional de Biodiversidad (Costa Rica), the Queensland National Parks and Wildlife Service, facilitated by R. Raven of the Queensland Museum (Queensland), Department of Primary Industries, Water and Environment Resource Management and Conservation Division, Wildlife Management Branch and Biodiversi1y Conservation Branch (Tasmania), Department of National Parks, Wildlife and Plant Conservation, the Queen Sirikit Botanic Garden, Maerim, Chiang Mai, and Danish International Development Assistance (DANIDA) (Thailand). In addition to those, the following persons helped to organize and provided essential support during fieldwork: Chaweewan Hutacharern, Prasit Wongprom, Krit Charonthong, and Suyanee Vessabutr (Thailand), Carlos Viquez (Costa Rica), Lisa Boutin, Robert Raven, and Barbara Baehr (Australia), Pablo Goloboff, Paula Cichero, Lara Lopardo, Julián Faivovich, Peter Michalik (Argentina), Norman Platnick, Kefyn Catley, and T. Allen (Chile), Tanza Crouch, Tharina Bird, and Matzaj Kuntner (South Africa). Pablo Goloboff provided extensive guidance with the phylogenetic analysis and the programming of scripts in TNT, a free program made available thanks to the Willi Hennig Society. This work was primarily funded by the generous support or a Fessenden Research Fellowship by the AMNH and an external postdoctoral fellowship from CONICET. Subsequent support was obtained from NSF (awards EAR-0228699 to Ward Wheeler, 0613754 to Norman Platnick, and 0956049 to Paula Mabee), CONICET (PEI 6558, PIP 6502, PIP 112-200801-03209), FONCyT (PICT 2003-14092, PICT 2007-01393), UBACyT 2010–2011 01/1240), and a visiting scholar award from NESCent. I owe special thanks to the team of my laboratory at MACN for their continuous support during the preparation of this work, particularly to Facundo Labarque, Matías Izquiero, Luis Piacentini, Andrés Ojanguren Affilastro, Gonzalo Rubio, and in particular Cristian Grismado. My wife, Paula, was the most encouraging and supportive, and made a beautiful time of our stay in New York and the following years during the preparation of this work.

REFERENCES

Álvarez-Padilla, F., and G. Hormiga. 2008. A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. Journal of Arachnology 35: 538–542.

Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zoological Journal of the Linnean Society 141: 447–626.

Agnarsson, I., J.A. Coddington, and L.J. May-Collado. 2008. Elongated pedicillate setae: a putative sensory system and synapomorphy of spiders. Journal of Arachnology 35: 411–426.

Arzt, E., S.N. Gorb, and R. Spolenak. 2003. From micro to nano contacts in biological attachment devices. Proceedings of the National Academy of Sciences of the United States of America 100: 10603–10606.

Baehr, M., and B. Baehr. 1993. The Hersiliidae of the Oriental Region including New Guinea. Taxonomy, phylogeny, zoogeography (Arachnida, Araneae). Spixiana (Supplement) 19: 1–96.

Baert, L. 2009. The genus *Odo* Keyserling, 1887 (Araneae: Zoridae) of the Galápagos islands (Ecuador). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie 79: 45–57.

Banks, N. 1892. A classification of North American spiders. Canadian Entomologist 24: 88–97.

Barth, F.G. 2002. A spider's world: senses and behavior. Berlin: Springer Verlag.

Barth, F.G., and W. Libera. 1970. Ein Atlas der Spaltsinnesorgane von *Cupiennius salei* Keys. Chelicerata (Araneae). Zeitschrift für Morphologie der Tiere 68: 343–369.

Baum, S. 1972. Zum "Cribellaten-problem": Die genitalstrukturen der Oecobiinae und Uroctei-nae (Arachnida: Araneae). Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins zu Hamburg N.F. 16: 101–153.

Baylis, H.A., and R. Daubney. 1926. A synopsis of the families and genera of Nematoda. London: British Museum (Natural History).

Benjamin, S.P. 2000. *Epidius parvati* sp. n., a new species of the genus *Epidius* from Sri Lanka (Araneae: Thomisidae). Bulletin of the British Arachnological Society 11: 284–288.

Benjamin, S.P. 2011. Phylogenetics and comparative morphology of crab spiders (Araneae: Dionycha, Thomisidae). Zootaxa 3080: 1–108.

Bennett, R.G. 1992. The spermathecal pores of spiders with special reference to dictynoids and amaurobioids (Araneae, Araneomorphae, Araneoclada). Proceedings of the Entomological Society of Ontario 123: 1–21.

Benoit, P.L.G. 1978. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles (Mission P.L.G. Benoit–J.J. Van Mol 1972). Oxyopidae, Zodariidae et Selenopidae (Araneae). Revue de Zoologie Africaine 92: 690–699.

Berg, L.S. 1940. Classification of fishes, both recent and fossil. Travaux de l'Institut Zoologique de l'Académie des Sciences de l'URSS 5: 87–517. [in Russian and English]

Beutel, R.G., and S.N. Gorb. 2001. Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. Journal of Zoological Systematics and Evolutionary Research 39: 177–207.

Blackledge, T.A., et al. 2009. Reconstructing web evolution and spider diversification in the molecular era. Proceedings of the National Academy of Sciences of the United States of America 106: 5229–5234.

Blest, A.D., D.C. O'Carroll, and M. Carter. 1990. Comparative ultrastructure of layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. Cell and Tissue Research 262: 445–460.

Bonaldo, A.B. 1994. A subfamilia Eutichurinae na região neotropical, com a revisão do gênero *Eutichurus* Simon, 1896 (Araneae, Miturgidae). Iheringia Série Zoologia 76: 101–159.

Bonaldo, A.B. 1997. On the new Neotropical spider genus *Ianduba* (Araneae, Corinnidae). Iheringia Série Zoologia 83: 165–180.

Bonaldo, A.B. 2000. Taxonomia da subfamília Corinninae (Araneae, Corinnidae) nas regiões neotropical e neártica. Iheringia Série Zoologia 89: 3–148.

Bonaldo, A.B., and A.D. Brescovit. 1992. As aranhas do gênero *Cheiracanthium* CL Koch, 1839 na região neotropical (Araneae, Clubionidae). Revista Brasileira de Entomologia 36: 731–740.

Bonaldo, A.B., R. Saturnino, M.J. Ramírez, and A.D. Brescovit. 2012. A revision of the American spider genus *Strotarchus* Simon, 1888 (Araneae: Dionycha, Systariinae). Zootaxa 3312: 1–44.

Bonnet, P. 1939. Elevage de *Filistata insidiatrix* (Araneide). Bulletin de la Societe d'Histoire Naturelle de Toulouse 73: 167–188.

Bonnet, P. 1956. Bibliographia araneorum. Toulouse: Les Frères Douladoure 2: 919–1926.

Bosselaers, J. 2002. A cladistic analysis of Zoropsidae (Araneae), with description of a new genus. Belgian Journal of Zoology 132: 141–154.

Bosselaers, J., and R. Jocqué. 2000. *Hortipes*, a huge genus of tiny Afrotropical spiders (Araneae, Liocranidae). Bulletin of the American Museum of Natural History 256: 1–108.

Bosselaers, J., and R. Jocqué. 2002. Studies in Corinnidae: cladistic analysis of 38 corinnid and liocranid genera, and transfer of Phrurolithinae. Zoologica Scripta 31: 241–270.

Bosselaers, J., and R. Jocqué. 2013. Studies in Liocranidae (Araneae): a new Afrotropical genus featuring a synapomorphy for the Cybaeodinae. European Journal of Taxonomy 40: 1–49.

Bosselaers, J., et al. 2010. High-resolution X-ray computed tomography of an extant new *Donuea* (Araneae: Liocranidae) species in Madagascan copal. Zootaxa 2427: 25–35.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Brescovit, A.D. 1997. Revisão de Anyphaeninae Bertkau a nível de gêneros na região neotropical (Araneae, Anyphaenidae). Revista Brasileira de Zoologia 13: 1–187.

Bristowe, W.S. 1938. The classification of spiders. Proceedings of the Zoological Society of London 108: 285–322.

Bristowe, W.S. 1941. The comity of spiders. London: Ray Society.

Buxton, B.H. 1913. Coxal glands of the arachnids. Zoologische Jahrbücher (Supplement) 14: 231–282.

Cambridge, F.O.P.-. 1893. Handbook to the study of British spiders (Drassidae and Agalenidae). British Naturalist (Suppl. 3): 117–170.

Carico, J.E., and P.C. Holt. 1964. A comparative study of the female copulatory apparatus of certain species in the spider genus *Dolomedes*. Technical Bulletin VA 5–27. Blacksburg: Virginia Agricultural Experiment Station.

Causard, M. 1896. Recherches sur l'appareil circulatoire des aranéides. Bulletin Scientifique de la France et de la Belgique 29: 1–109.

Coddington, J.A. 1986. The genera of the spider family Theridiosomatidae. Smithsonian Contributions to Zoology 422: 1–96.

Coddington, J.A. 1989. Spinneret silk spigot morphology: evidence for the monophyly of orbweaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. Journal of Arachnology 17: 71–95.

Coddington, J.A. 1990. Ontogeny and homology in the male palpus of orb weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496: 1–52.

Coddington, J.A., G. Giribet, M.S. Harvey, L. Prendini, and D.E. Walter. 2004. Arachnida. *In* J. Cracraft and M.J. Donoghue (editors), Assembling the tree of life. Oxford: Oxford University Press.

Compagnucci, L.A., and M.J. Ramírez. 2000. A new species of the spider genus *Naevius* Roth from Argentina (Araneae, Amaurobiidae, Macrobuninae). Studies in Neotropical Fauna and Environment 35: 203–207.

Corronca, J.A. 1997. The genus *Selenops* (Araneae, Selenopidae) from South America: description of new species. Iheringia Série Zoologia 82: 75–80.

Crome, W. 1955. Die Beziehungen zwischen dem dorsalen Zeichnungsmuster und der Metamerie des Spinnenabdomens, II. Zoologische Jahrbuecher Systematik 83: 541–638.

Cushing, P.E. 1997. Myrmecomorphy and myrmecophily in spiders: a review. Florida Entomologist 80: 165–193.

Dacke, M., et al. 1999. Built-in polarizers form part of a compass organ in spiders. Nature 401: 470–474.

Dacke, M., T.-A. Doan, and D.-C. O'Carroll. 2001. Polarized light detection in spiders. Journal of Experimental Biology 204: 2481–2490.

Dahl, F. 1908. Die Lycosiden oder Wolfsspinnen Deutschlands und ihre Stellung im Haushalt der Natur. Nach statistichen Untersuchungen dargestellt. Nova Acta Academiae Caesareae Leopoldino-Carolinae 88: 175–678.

Davies, V.T. 1998. A revision of the Australian metaltellines (Araneae: Amaurobioidea: Amphiectidae: Metaltellinae). Invertebrate Taxonomy 12: 211–243.

Davies, V.T. 1999. *Carbinea*, a new spider genus from north Queensland, Australia (Araneae, Amaurobioidea, Kababininae). Journal of Arachnology 27: 25–36.

Deeleman-Reinhold, C.L. 2001. Forest spiders of South East Asia: with a revision of the sac and ground spiders (Araneae: Clubionidae, Corinnidae, Liocranidae, Gnaphosidae, Prodidomidae and Trochanterriidae [sic]), Leiden: Brill.

Demir, H., M. Aktaş, and O. Seyyar. 2008. The female of *Xysticus pseudorectilineus* (Wunderlich, 1995) (Araneae: Thomisidae) from Turkey. Zootaxa 1674: 65–68.

di Caporiacco, L. 1938. II sistema degli Araneidi. Archivio Zoologico Italiano, Supplement Attualita Zoologiche 254: 35–155.

Dippenaar-Schoeman, A.S., and R. Jocqué. 1997. African spiders: an identification manual. Handbook no. 9. Pretoria: Plant Protection Research Institute.

Duncan, R.P., K. Autumn, and G.J. Binford. 2007. Convergent setal morphology in sand-covering spiders suggests a design principle for particle capture. Proceedings of the Royal Society B, Biological Sciences 274: 3049–3057.

Dunlop, J.A. 1996. Evidence for a sister group relationship between Ricinulei and Trigonotarbida. Bulletin of the British Arachnological Society 10: 193–204.

Eberhard, W.G. 1988. Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic implications. Bulletin of the British Arachnological Society 7: 247–251.

Filippov, A., V.L. Popov, and S.N. Gorb. 2011. Shear induced adhesion: contact mechanics of biological spatula-like attachment devices. Journal of Theoretical Biology 276: 126–131.

Foelix, R.F. 1970a. Chemosensitive hairs in spiders. Journal of Morphology 132: 313–333.

Foelix, R.F. 1970b. Structure and function of tarsal sensilla in the spider *Araneus diadematus*. Journal of Experimental Zoology 175: 99–108.

Foelix, R. 2011. Biology of spiders, 3rd ed. Oxford: Oxford University Press.

Foelix, R.F., and H. Jung. 1978. Some anatomical aspects of *Hypochilus thorelli* with special reference to the calamistrum and cribellum.

Symposia of the Zoological Society of London 42: 417–422.

Forster, R.R. 1955. A new family of spiders of the sub-order Hypochilomorphae. Pacific Science 9: 277–285.

Forster, R.R. 1970. The spiders of New Zealand. Part III. Otago Museum Bulletin 3: 1–184.

Forster, R.R., and A.D. Blest. 1979. The spiders of New Zealand, part V. Cycloctenidae, Gnaphosidae, Clubionidae, Linyphiidae – Mynogleninae. Otago Museum Bulletin 5: 1–173.

Forster, R.R., and N.I. Platnick. 1984. A review of the archaeid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). Bulletin of the American Museum of Natural History 178 (1): 1–106.

Forster, R.R., and C.L. Wilton. 1973. The spiders of New Zealand. Part IV. Otago Museum Bulletin 4: 1–309.

Forster, R.R., N.I. Platnick, and M.R. Gray. 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae, Araneomorphae). Bulletin of the American Museum of Natural History 185 (1): 1–116.

Galiano, M.E. 1962. Redescripciones de especies del género *Lyssomanes* Hentz, 1845, basadas en los ejemplares típicos. Descripción de una especie nueva (Araneae, Salticidae). Acta Zoológica Lilloana 18: 45–97.

Galiano, M.E. 1980. Revisión del género *Lyssomanes* Hentz, 1845 (Araneae, Salticidae). Opera Lilloana 30: 1–104.

Giribet, G. 2003. Stability in phylogenetic formulations and its relationship to nodal support. Systematic Biology 52: 554–564.

Giribet, G., G.D. Edgecombe, and W.C. Wheeler. 2001. Arthropod phylogeny based on eight molecular loci and morphology. Nature 413: 157–161.

Goloboff, P.A. 1993. Estimating character weights during tree search. Cladistics 9: 83–91.

Goloboff, P.A. 1997. Self-weighted optimization: tree searches and character state reconstructions under implied transformation costs. Cladistics 13: 225–245.

Goloboff, P.A. 2000. The family Gallieniellidae (Araneae, Gnaphosoidea) in the Americas. Journal of Arachnology 28: 1–6.

Goloboff, P.A., and J.S. Farris. 2001. Methods for quick consensus estimation. Cladistics 17: S26–S34.

Goloboff, P.A., et al. 2003. Improvements to resampling measures of group support. Cladistics 19: 324–332.

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2008a. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.

Goloboff, P.A., J.M. Carpenter, J.S. Arias, and D.R. Miranda Esquivel. 2008b. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. Cladistics 24: 1–16.

Goloboff, P.A., C.I. Mattoni, and A.S. Quinteros. 2006. Continuous characters analyzed as such. Cladistics 22: 589–601.

Gorb, S.N. 2008. Biological attachment devices: exploring nature's diversity for biomimetics. Philosophical Transactions of the Royal Society A, Mathematical, Physical and Engineering Sciences 366: 1557–1574.

Gorb, S.N., and F.G. Barth. 1996. A new mechanosensory organ on the anterior spinnerets of the spider *Cupiennius salei* (Araneae, Ctenidae). Zoomorphology 116: 7–14.

Gray, M.R. 1995. Morphology and relationships within the spider family Filistatidae (Araneae: Araneomorphae). Records of the Western Australian Museum Supplement 52: 79–89.

Gray, R.G., and H.M. Smith. 2004. The "striped" group of stiphidiid spiders: two new genera from northeastern New South Wales, Australia (Araneae: Stiphidiidae: Amaurobioidea). Records of the Australian Museum 56: 123–138.

Gray, R.G., and H.M. Smith. 2008. A new subfamily of spiders with grate-shaped tapeta from Australia and Papua New Guinea (Araneae: Stiphidiidae: Borralinae). Records of the Australian Museum 60: 13–44.

Griswold, C.E. 1991. A revision and phylogenetic analysis of the spider genus *Machadonia* Lehtinen (Araneae, Lycosoidea). Entomologica Scandinavica 22: 305–352.

Griswold, C.E. 1993. Investigations into the phylogeny of the lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). Smithsonian Contributions to Zoology 539: 1–39.

Griswold, C.E. 1994. A revision and phylogenetic analysis of the spider genus *Phanotea* Simon (Araneae, Lycosoidea). Annalen Zoologische Wetenschappen 273: 1–83.

Griswold, C.E. 2002. A revision of the African spider genus *Raecius* Simon, 1892 (Araneae, Zorocratidae). Proceedings of the California Academy of Sciences 53: 117–149.

Griswold, C.E., J.A. Coddington, G. Hormiga, and N. Scharff. 1998. Phylogeny of the orb-web building spiders. Zoological Journal of the Linnean Society 123: 1–99.

Griswold, C.E., J.A. Coddington, N.I. Platnick, and R.R. Forster. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). Journal of Arachnology 27: 53–63.

Griswold, C.E., M.J. Ramírez, J.A. Coddington, and N.I. Platnick. 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae, Araneomorphae, Entelegynae) with comments on their phylogeny. Proceedings of the California Academy of Sciences, 4th Series 56: 1–324.

Griswold, C.E., T. Audisio, and J.M. Ledford. 2012. An extraordinary new family of spiders from caves in the Pacific Northwest (Araneae, Trogloraptoridae, new family). ZooKeys 215: 77–102.

Haddad, C.R. 2005. A re-description of *Corinna natalis* Pocock, 1898 (Araneae, Corinnidae), Africa's largest dark sac spider, with natural history notes. Journal of Afrotropical Zoology 2: 27–32.

Haddad, C.R. 2006. *Spinotrachelas*, a new genus of tracheline sac spiders from South Africa (Araneae: Corinnidae). African Invertebrates 47: 85–93.

Haddad, C.R., and R. Lyle. 2008. Three new genera of tracheline sac spiders from southern Africa (Araneae: Corinnidae). African Invertebrates 49: 37–76.

Haddad, C.R., R. Lyle, J. Bosselaers, and M.J. Ramírez. 2009. A revision of the endemic South African spider genus *Austrachelas*, with its transfer to the Gallieniellidae (Arachnida: Araneae). Zootaxa 2296: 1–38.

Harms, D., and M.S. Harvey. 2009. A review of the pirate spiders of Tasmania (Arachnida, Mimetidae, *Australomimetus*) with description of a new species. Journal of Arachnology 37: 188–205.

Harvey, M.S. 1995. The systematics of the spider family Nicodamidae (Araneae: Amaurobioidea). Invertebrate Taxonomy 9: 279–386.

Henschel, J.R., V.T. Davies, and C.R. Dickman. 1995. The slit spider (Araneae: Clubionoidea) that constructs fissures in the sand dunes of the Simpson desert, central Australia. Journal of Natural History 29: 137–145.

Hill, D.E. 1977. The pretarsus of salticid spiders. Zoological Journal of the Linnean Society 60: 319–338.

Hill, D.E. 1979. The scales of salticid spiders. Zoological Journal of the Linnean Society 65: 193–218.

Hill, D.E. 2006. Jumping spider feet (Araneae, Salticidae). Version 3. Peckhamia Epublications. Online resource (http://peckhamia.com/epublications.html), accessed 16 April 2012.

Hill, D.E. 2009. Euophryine jumping spiders that extend their third legs during courtship (Araneae: Salticidae: Euophryinae: *Maratus, Saitis*). Peckhamia 74.1: 1–27.

Hill, D.E., and D.B. Richman. 2009. The evolution of jumping spiders (Araneae: Salticidae): a review. Peckhamia 75.1: 1–7.

Homann, H. 1951. Die Nebenaugen der Araneen. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 71: 56–144.

Homann, H. 1968. Die Stellung der Cycloctenidae im System der Aranee. Senkenbergiana Biologica 49: 51–57.

Homann, H. 1971. Die Augen der Araneae: Anatomie, Ontogenie und Bedeutung für die Systematik (Chelicerata Arachnida). Zeitschrift für Morphologie der Tiere 69: 201–272.

Homann, H. 1975. Die Stellung der Thomisidae und der Philodromidae im System der Araneae (Chelicerata, Arachnida). Zeitschrift für Morphologie der Tiere 80: 181–202.

Homann, H. 1985. Die Cheliceren der Araneae, Amblypygi, und Uropygi mit den Skleriten, den Plagulae (Chelicerata, Arachnomorpha). Zoomorphologie 105: 69–75.

Huber, B.A. 1994. Genital bulb muscles in entelegyne spiders. Journal of Arachnology 22: 75–76.

Huber, B.A. 1995a. The retrolateral tibial apophysis in spiders – shaped by sexual selection? Zoological Journal of the Linnean Society 113: 151–163.

Huber, B.A. 1995b. Genital morphology and copulatory mechanics in *Anyphaena accentuata* (Anyphaenidae) and *Clubiona pallidula* (Clubionidae: Araneae). Journal of Zoology (London) 235: 689–702.

Huber, B.A. 2004. Evolutionary transformation from muscular to hydraulic movements in spider (Arachnida, Araneae) genitalia: a study based on histological serial sections. Journal of Morphology 261: 364–376.

Izquierdo, M.A., and F.M. Labarque. 2010. Description of the female of *Orsolobus pucara* Forster & Platnick 1985, with comments on the functional morphology of the female genitalia in Dysderoidea (Araneae: Dysderoidea: Orsolobidae). Journal of Arachnology 38: 511–520.

Izquierdo, M.A., and M.J. Ramírez. 2008. Two new spider species of the genera *Aysenia* and *Aysenoides* from southern Chile and Argentina: description and phylogenetic relationships (Araneae: Anyphaenidae, Amaurobioidinae). Zootaxa 1861: 29–43.

Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201: 1–160.

Jocqué, R., and R. Bosmans. 1989. A revision of the genus *Storenomorpha* Simon (Araneae, Zodariidae). Spixiana 12: 125–134.

Jocqué, R., and S.A. Dippenaar-Schoeman. 2006. Spider families of the world. Tervuren, Belguim: Royal Museum for Central Africa.

Jäger, P. 2001. Diversität der Riesenkrabbenspinnen im Himalaya—die Radiation zweier Gattungen in den Schneetropen (Araneae, Sparassidae, Heteropodinae). Courier Forschungsinstitut Senckenberg 232: 1–136.

Jäger, P., and H. Ono. 2000. Sparassidae of Japan. I. New species of *Olios*, *Heteropoda*, and *Sinopoda*, with notes on some known species (Araneae: Sparassidae: Sparassinae and Heteropodinae). Acta Arachnologica (Tokyo) 49: 41–60.

Kovoor, J. 1977. La soie et les glandes séricigènes des arachnides. Annales de Biologie 16: 97–141.

Kovoor, J., and H.M. Peters. 1988. The spinning apparatus of *Polenecia producta* (Araneae: Uloboridae): structure and histochemistry. Zoomorphology 108: 47–60.

Kraus, O. 1975. Phylogeny and systematics of higher taxa in spiders: open problems and present approach. *In* Proceedings of the 6th International Arachnonology Congress, Amsterdam: 7–11. Amsterdam: Nederlandse Entomologische Verenigung.

Kropf, C. 1990. *Comaroma* is an anapid spider (Arachnida, Araneae, Anapidae). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 31–32: 185–204.

Lamy, E. 1902. Recherches anatomiques sur les trachées des araignées. Annales des Sciences Naturelles, Zoologie 15: 149–280.

Land, M.F. 1969. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. Journal of Experimental Biology 51: 471–493.

Land, M.F. 1985. The morphology and optics of spider eyes. *In* F.G. Barth (editor), Neurobiology of arachnids, 53–78. Berlin: Springer Verlag.

Ledford, J.M., and C.E. Griswold. 2010. A study of the subfamily Archoleptonetinae (Araneae, Leptonetidae) with a review of the morphology and relationships for the Leptonetidae. Zootaxa 2391: 1–32.

Leech, R.E. 1972. A revision of the Nearctic Amaurobiidae (Arachnida: Araneida). Memoirs of the Entomological Society of Canada 84: 1–187.

Lehtinen, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Annales Zoologici Fennici 4: 199–467.

Lehtinen, P.T. 1975. Notes on the phylogenetic classification of Araneae. *In* Proceedings of the 6th International Arachnonogy Congress, Amsterdam, 26–29. Amsterdam: Nederlandse Entomologische Verenigung.

Lehtinen, P. 1996. The ultrastructure of leg skin in the phylogeny of spiders. Revue Suisse de Zoologie, hors série 2: 399–421.

Levi, H.W. 1982. The spider genera *Psechrus* and *Fecenia* (Araneae: Psechridae). Pacific Insects 24: 114–138.

Levy, G. 1999. Spiders of the genera *Anagraphis* and *Talanites* (Araneae, Gnaphosidae) from Israel. Israel Journal of Zoology 45: 215–225.

Lopardo, L., and G. Hormiga. 2007. On the synaphrid spider *Cepheia longiseta* (Simon 1881) (Araneae, Synaphridae). American Museum Novitates 3575: 1–18.

Lopardo, L., and G. Hormiga. 2008. Phylogenetic placement of the Tasmanian spider *Acrobleps hygrophilus* (Araneae, Anapidae) with comments on the evolution of the capture web in Araneoidea. Cladistics 24: 1–33.

Lopardo, L., and M.J. Ramírez. 2007. The combing of cribellar silk by the prithine *Misionella mendensis,* with notes on other filistatid spiders (Araneae: Filistatidae). American Museum Novitates 3563: 1–14.

Lopardo, L., M.J. Ramírez, C.J. Grismado, and L.A. Compagnucci. 2004. Web building behavior and the phylogeny of austrochiline apiders. Journal of Arachnology 32: 42–54.

Lopardo, L., G. Giribet, and G. Hormiga. 2011. Morphology to the rescue: molecular data and the signal of morphological characters in combined phylogenetic analyses—a case study from mysmenid spiders (Araneae, Mysmenidae), with comments on the evolution of web architecture. Cladistics 27: 278–330.

Lotz, L.N., and A.S. Dippenaar-Schoeman. 1999. *Cheiramiona*, a new Afrotropical spider genus (Araneae: Miturgidae: Eutichurinae). Navorsinge van die Nasionale Museum (Bloemfontein, South Africa) 15: 29–44.

Maddison, W.P. 1988. A revision of jumping spider species groups formerly placed in the genus *Metaphidippus*, with a discussion of salticid phylogeny (Araneae). Ph.D. dissertation, Harvard University.

Maddison, W.P. 1996. *Pelegrina* Franganillo and other jumping spiders formerly placed in the genus *Metaphidippus* (Araneae: Salticidae). Bulletin of the Museum of Comparative Zoology 154: 215–368.

Maddison, W.P. 2009. New cocalodine jumping spiders from Papua New Guinea (Araneae: Salticidae: Cocalodinae). Zootaxa 2021: 1–22.

Maddison, W.P., and M.C. Hedin. 2003. Jumping spider phylogeny (Araneae: Salticidae). Invertebrate Systematics 17: 529–549.

Maddison, W.P., and K. Needham. 2006. Lapsiines and hisponines as phylogenetically basal salticid spiders (Araneae: Salticidae). Zootaxa 1255: 37–55.

Maddison, W.P., M.R. Bodner, and K.M. Needham. 2008. Salticid spider phylogeny revisited, with the discovery of a large Australasian clade (Araneae: Salticidae). Zootaxa 1893: 49–64.

Marples, B.J. 1967. The spinnerets and epiandrous glands of spiders. Journal of the Linnean Society, Zoology 46: 209–222.

Marples, B.J. 1968. The hypochilomorph spiders. Proceedings of the Linnean Society of London 179: 11–31.

Marples, B.J. 1983. Observations on the structure of the fore-gut of spiders. Bulletin of the British Arachnological Society 6: 46–52.

Marusik, Y.M., and M.M. Kovblyuk. 2011. Spiders of Siberia and Russian far east. Moscow: KMK Press. [in Russian]

Michalik, P., W. Reiher, M. Tintelnot-Suhm, F.A. Coyle, and G. Alberti. 2005. Female genital system of the folding-trapdoor spider *Antrodiaetus unicolor* (Hentz, 1842) (Antrodiaetidae, Araneae): ultrastructural study of form and function with notes on reproductive biology of spiders. Journal of Morphology 263: 284–309.

Miller, J.A., C.E. Griswold, and C.M. Yin. 2009. The symphytognathoid spiders of the Gaoligongshan, Yunnan, China (Araneae, Araneoidea): systematics and diversity of micro-orbweavers. ZooKeys 11: 9–195.

Miller, J.A., et al. 2010. Phylogeny of entelegyne spiders: affinities of the family Penestomidae (new rank), generic phylogeny of Eresidae, and asymmetric rates of change in spinning organ evolution (Araneae, Araneoidea, Entelegynae). Molecular Phylogenetics and Evolution 55: 786–804.

Millot, J. 1930. Glandes venimeuses et glandes séricigènes chez les sicariides. Bulletin de la Société Zoologique de France 55: 150–175.

Millot, J. 1931a. Les glandes venimeuses des araneides. Annales des Sciences Naturelles, Zoologie 14: 113–147.

Millot, J. 1931b. Les diverticules intestinaux du cephalothorax chez les Araignées vraies. Zeitschrift für Morphologie und Ökologie der Tiere 21: 740–764.

Millot, J. 1931c. La metamerisation postembryonnaire des jeunes Araignées. Bulletin de la Société Zoologique de France 56: 140–145.

Millot, J. 1933a. L'anatomie interne des dinopides. Bulletin de la Société Zoologique de France 57: 537–542.

Millot, J. 1933b. Notes complementaires sur l'anatomie des liphistiides et des hypochilides, à propos d'un travail recent de A. Petrunkevitch. Bulletin de la Société Zoologique de France 58: 217–235.

Millot, J. 1933c. Position systematique des araignées du genre *Liphistius*, d'après leur anatomie interne. Comptes Rendus de l'Académie des Sciences 196: 129–130.

Millot, J. 1936. Metamerisation et musculature abdominale chez les aranéomorphes. Bulletin de la Société Zoologique de France 61: 181–204.

Millot, J. 1938. L'appareil séricegène d'*Oecobius cellariorum* Dugès, suivi de quelques considérations générales sur les glandes sécrétrices de soie des aranéides. Travaux de la Station Zoologique de Wimerenx 13: 479–487.

Millot, J. 1948. Faits nouveaux concernant les *Archaea* [aranéides]. Mémoires de l'Institut Scientifique de Madagascar, Série A: Biologie Animale 1: 3–14.

Millot, J. 1949. Ordre des aranéides (Araneae). *In* P. Grassé (editor), Traite de Zoologie 6: 589–743. Paris: Masson.

Murphy, J. 2007. Gnaphosid genera of the world. St Neots, Cambridgeshire: British Arachnological Society.

Muster, C. 2009a. The *Ebo*-like running crab spiders in the Old World (Araneae, Philodromidae). ZooKeys 16: 43–73.

Muster, C. 2009b. Phylogenetic relationships within Philodromidae, with a taxonomic revision of *Philodromus* subgenus *Artanes* in the western Palearctic (Arachnida: Araneae). Invertebrate Systematics 23: 135–169.

Nixon, K.C. 1999. Winclada (version 1.00.04). Ithaca, NY: Published by the author.

Nørgaard, T., D.-E. Nilsson, J.R. Henschel, A. Garm, and R. Wehner. 2008. Vision in the nocturnal wandering spider *Leucorchestris arenicola* (Araneae: Sparassidae). Journal of Experimental Biology 211: 816–823.

Oliveira, P.S., and I. Sazima. 1984. The adaptive bases of ant-mimicry in a Neotropical aphantochilid spider (Araneae: Aphantochilidae). Biological Journal of the Linnean Society 22: 145–155.

Oliveira, P.S., and I. Sazima. 1985. Ant-hunting behaviour in spiders with emphasis on *Strophius nigricans* (Thomisidae). Bulletin of the British Arachnological Society 6: 309–312.

Ono, H. 1988. A revisional study of the spider family Thomisidae (Arachnida, Araneae) of Japan. Tokyo: National Science Museum.

Ono, H. 2009. The spiders of Japan with keys to the families and genera and illustrations of the species. Kanagawa: Tokai University Press. [in Japanese]

Opell, B.D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bulletin of the Museum of Comparative Zoology 148: 443–549.

Parry, D.A. 1957. Spider leg-muscles and the autotomy mechanism. Quarterly Journal of Microscopical Science 98: 331–340.

Penniman, A.J. 1985. Revision of the *britcheri* and *pugnata* groups of *Scotinella* (Araneae, Corinnidae, Phrurolithinae) with a reclassification of phrurolithine spiders. Ph.D. dissertation, Ohio State University.

Peters, H.M. 1992. On structure and construction of capture threads by cribellate spiders of the Eresidae family (Arachnida, Araneae). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 33: 213–227.

Petrunkevitch, A. 1928. Systema aranearum. Transactions of the Connecticut Academy of Arts and Sciences 29: 1–270.

Petrunkevitch, A. 1933. An inquiry into the natural classification of spiders, based on a study of their internal anatomy. Transactions of the Connecticut Academy of Arts and Sciences 31: 303–389.

Petrunkevitch, A. 1939. The status of the family Archaeidae and the genus *Landana*. Annals of the Entomologcial Socety of America 32: 479–501.

Platnick, N.I. 1974. The spider family Anyphaenidae in America, north of Mexico. Bulletin of the Museum of Comparative Zoology 146: 205–266.

Platnick, N.I. 1976. Notes on the spider genus *Doliomalus* (Araneae: Gnaphosidae). Revue de Zoologie Afrcaine 90: 975–983.

Platnick, N.I. 1986. A review of the spider genus *Cyrioctea* (Araneae, Zodariidae). American Museum Novitates 2858: 1–9.

Platnick, N.I. 1990. Spinneret morphology and the phylogeny of ground spiders (Araneae, Gnaphosoidea). American Museum Novitates 2978: 1–42.

Platnick, N.I. 1991. A revision of the ground spider family Cithaeronidae (Araneae, Gnaphosoidea). American Museum Novitates 3018: 1–13.

Platnick, N.I. 1999. A revision of the Appalachian spider genus *Liocranoides* (Araneae: Tengellidae). American Museum Novitates 3285: 1–13.

Platnick, N.I. 2000. A relimitation and revision of the Australasian ground spider family Lamponidae (Araneae: Gnaphosoidea). Bulletin of the American Museum of Natural History 245: 1–330.

Platnick, N.I. 2002. A revision of the Australasian ground spiders of the families Ammoxenidae, Cithaeronidae, Gallieniellidae, and Trochanteriidae (Araneae: Gnaphosoidea). Bulletin of the American Museum of Natural History 271: 1–243.

Platnick, N.I. 2012. The world spider catalog, version 12.5. New York: American Museum of Natural History. Internet resource (http://research.amnh.org/iz/spiders/catalog), accessed 5 June 5 2012. [doi: 10.5531/db.iz.0001]

Platnick, N.I., and B. Baehr. 2006. A revision of the Australasian ground spiders of the family Prodidomidae (Araneae: Gnaphosoidea). Bulletin of the American Museum of Natural History 298: 1–287.

Platnick, N.I., and R.L.C. Baptista. 1995. On the spider genus *Attacobius* (Araneae, Dionycha). American Museum Novitates 3120: 1–9.

Platnick, N.I., and A.B. Bonaldo. 1995. On the spider genus *Hebrithele* (Araneae, Miturgidae). Journal of Arachnology 23: 13–16.

Platnick, N.I., and N. Dupérré. 2010. The Andean goblin spiders of the new genera *Niarchos* and *Scaphios* (Araneae, Oonopidae). Bulletin of the American Museum of Natural History 345: 1–120.

Platnick, N.I., and C. Ewing. 1995. A revision of the tracheline spiders (Araneae, Corinnidae) of southern South America. American Museum Novitates 3128: 1–41.

Platnick, N.I., and R.R. Forster. 1993. A revision of the New Caledonian spider genus *Bradystichus* (Araneae, Lycosoidea). American Museum Novitates 3075: 1–14.

Platnick, N.I., and E. Griffin. 1990. On *Rastellus*, a new genus of the spider family Ammoxenidae (Araneae, Gnaphosoidea). American Museum Novitates 2995: 1–11.

Platnick, N.I., and D. Penney. 2004. A revision of the widespread spider genus *Zimiris* (Araneae, Prodidomidae). American Museum Novitates 3450: 1–12.

Platnick, N.I., and M.U. Shadab. 1974. A revision of the *tranquillus* and *speciosus* groups of the spider genus *Trachelas* (Araneae, Clubionidae) in North and Central America. American Museum Novitates 2553: 1–34.

Platnick, N.I., and M.U. Shadab. 1975. A revision of the spider genus *Gnaphosa* (Araneae, Gnaphosidae) in America. Bulletin of the American Museum of Natural History 155 (1): 1–66.

Platnick, N.I., and M.U. Shadab. 1976. A revision of the spider genera *Lygromma* and *Neozimiris* (Araneae, Gnaphosidae). American Museum Novitates 2598: 1–23.

Platnick, N.I., and M.U. Shadab. 1989. A review of the spider genus *Teminius* (Araneae, Miturgidae). American Museum Novitates 2963: 1–12.

Platnick, N.I., and M.U. Shadab. 1993. A review of the pirate spiders (Araneae, Mimetidae) of Chile. American Museum Novitates 3074: 1–30.

Platnick, N.I., and D. Ubick. 1989. A revision of the spider genus *Drassinella* (Araneae, Liocranidae). American Museum Novitates 2937: 1–12.

Platnick, N.I., and D. Ubick. 2007. A revision of the spider genus *Zorocrates* Simon (Araneae, Zorocratidae). American Museum Novitates 3579: 1–44.

Platnick, N.I., J.A. Coddington, R.R. Forster, and C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016: 1–73.

Platnick, N.I., C.J. Grismado, and M.J. Ramírez. 1999. On the genera of the spider subfamily Otiothopinae (Araneae, Palpimanidae). American Museum Novitates 3257: 1–25.

Platnick, N.I., M.U. Shadab, and L.N. Sorkin. 2005. On the Chilean spiders of the family Prodidomidae (Araneae, Gnaphosoidea), with a revision of the genus *Moreno* Mello-Leitão. American Museum Novitates 3499: 1–31.

Platnick, N.I., et al. 2012. Tarsal organ morphology and the phylogeny of goblin spiders (Araneae, Oonopidae), with notes on basal genera. American Museum Novitates 3736: 1–52.

Polotow, D., and A.D. Brescovit. 2010. Phylogenetic relationships of the Neotropical spider genus *Itatiaya* (Araneae). Zoologica Scripta 40: 187–193.

Purcell, W.F. 1909. Development and origin of the respiratory organs in Araneae. Quarterly Journal of Microscopical Science 54: 1–110.

Purcell, W.F. 1910. The phylogeny of trachea in Araneae. Quarterly Journal of Microscopical Science 54: 519–563.

Rainbow, W.J. 1920. Arachnida from Lord Howe and Norfolk islands. Records of the South Australian Museum 1: 229–272.

Ramírez, M.J. 1993. Revisión del género *Liparotoma* Simon, 1884 (Araneae, Anyphaenidae). Boletin de la Sociedad de Biología de Concepción 64: 195–207.

Ramírez, M.J. 1995. A phylogenetic analysis of the subfamilies of Anyphaenidae (Arachnida, Araneae). Entomologica Scandinavica 26: 361–384.

Ramírez, M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). Journal of Arachnology 28: 149–157.

Ramírez, M.J. 2003. The spider subfamily Amaurobioidinae (Araneae, Anyphaenidae): a phylogenetic revision at the generic level. Bulletin of the American Museum of Natural History 277: 1–262.

Ramírez, M.J. 2007. Homology as a parsimony problem: a dynamic homology approach for morphological data. Cladistics 23: 588–612.

Ramírez, M.J. 2011. Spider ontology, version 0.9.8 beta. OBO Foundry. Internet resource (http://purl.bioontology.org/ontology/SPD), accessed 19 May 2012.

Ramírez, M.J. Submitted. Data from: The morphology and phylogeny of dionychan spiders (Araneae: Araneomorphae). Dryad Digital Repository. [doi:10.5061/dryad.p7d7c]

Ramírez, M.J., and C.J. Grismado. 1997. A review of spider family Filistatidae in Argentina (Arachnida, Araneae), with a cladistic reanalysis of filistatid genera. Entomologica Scandinavica 28: 319–349.

Ramírez, M.J., A.B. Bonaldo, and A.D. Brescovit. 1997. Revisión del género *Macerio* y comentarios sobre la ubicación de *Cheiracanthium, Tecution* y *Helebiona* (Araneae, Miturgidae, Eutichurinae). Iheringia, Série Zoologia 82: 43–66.

Ramírez, M.J., L. Lopardo, and A.B. Bonaldo. 2001. A review of the Chilean spider genus *Olbus*, with notes on the relationships of the Corinnidae (Arachnida, Araneae). Insect Systematics and Evolution 31: 441–462.

Ramírez, M.J., et al. 2007. Linking of digital images to phylogenetic data matrices using a morphological ontology. Systematic Biology 56: 283–294.

Raven, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bulletin of the American Museum of Natural History 182 (1): 1–180.

Raven, R.J. 1986. A cladistic reassessment of mygalomorph spider families (Araneae). *In* W.C. Eberhard, Y.D. Lubin, and B.C. Robinson (editors), Proceedings of the Ninth International Congress of Arachnology, Panama 1983: 223–227. Washington, D.C.: Smithsonian Institution Press.

Raven, R.J. 2008. Revisions of Australian ground-hunting spiders: III. *Tuxoctenus* gen. nov. (Araneomorphae: Zoridae). Records of the Western Australian Museum 24: 351–361.

Raven, R.J. 2009. Revisions of Australian ground-hunting spiders: IV. The spider subfamily Diaprograptinae subfam. nov. (Araneomorphae: Miturgidae). Zootaxa 2035: 1–40.

Raven, R.J. 2012. Revisions of Australian ground-hunting spiders. V. A new lycosoid genus from eastern Australia (Araneae: Tengellidae). Zootaxa 3305: 28–52.

Raven, R.J., K. Stumkat, and K. 2003. Problem solving in the spider families Miturgidae, Ctenidae and Psechridae (Araneae) in Australia and New Zealand. Journal of Arachnology 31: 105–121.

Raven, R.J., and K. Stumkat. 2005. Revisions of Australian ground-hunting spiders: II. Zoropsidae (Lycosoidea: Araneae). Memoirs of the Queensland Museum 50: 347–423.

Reiskind, J. 1969. The spider subfamily castianeirinae of North and Central America (Araneae, Clubionidae). Bulletin of the Museum of Comparative Zoology 138: 163–325.

Rheims, C. 2007. Análise cladística dos gêneros de Sparassidae Bertkau (Arachnida, Araneae). Ph.D. dissertation, Instituto de Biociências, Universidade de São Paulo.

Rix, M.G., M.S. Harvey, and J.D. Roberts. 2008. Molecular phylogenetics of the spider family Micropholcommatidae (Arachnida: Araneae) using nuclear rRNA genes (18s and 28s). Molecular Phylogenetics and Evolution 46: 1031–1048.

Rodrigo, A.G., and R.R. Jackson. 1992. Four jumping spider genera of the *Cocalodes*-group are monophyletic with genera of the Spartaeinae (Araneae: Salticidae). New Zealand Natural Sciences 19: 61–67.

Roewer, C.F. 1955. Katalog der Araneae von 1758 bis 1940, bzw. 1954., vol. 1. Bremen: Kommissions-Verlag von "Natura" in Bremen.

Santos, A.J., É.S. Álvares, and A.D. Brescovit. 2003. On the third valid species of the genus *Aglaoctenus* Tullgren (Araneae, Lycosidae). Revista Ibérica de Aracnología 8: 89–92.

Santos, A.D., and A.D. Brescovit. 2001. A revision of the South American spider genus *Aglaoctenus* Tullgren, 1905 (Araneae, Lycosidae, Sosippinae). Andrias 15: 75–90.

Scharff, N., and J.A. Coddington. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zoological Journal of the Linnean Society 120: 355–434.

Schütt, K. 2000. The limits of the Araneoidea (Arachnida: Araneae). Australian Journal of Zoology 48: 135–153.

Schütt, K. 2002. The limits and phylogeny of the Araneoidea (Arachnida, Araneae). Ph.D. dissertation, Humboldt-Universität zu Berlin.

Schütt, K. 2003. Phylogeny of Symphytognathidae s.l. (Araneae, Araneoidea). Zoologica Scripta 32: 129–151.

Scioscia, C.L. 1982. Evolución de la tricobotriotaxia durante el desarrollo de *Polybetes pythagoricus* (Holmberg, 1874). Revista de la Sociedad Entomológica Argentina 39: 207–219.

Shear, W.A. 1967. Expanding the palpi of male spiders. Breviora 259: 1–27.

Shear, W.A., P.A. Selden, W.D.I. Rolfe, P.M. Bonamo, and J.D. Grierson. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York. American Museum Novitates 2901: 1–74.

Sierwald, P. 1989. Morphology and ontogeny of female copulatory organs in American Pisauridae, with special reference to homologous features (Arachnida, Araneae). Smithsonian Contributions to Zoology 484: 1–24.

Sierwald, P. 1990. Morphology and homologous features in the male palpal organ in Pisauridae and other spider families, with notes on the taxonomy of Pisauridae (Arachnida: Araneae). Nemouria 35: 1–59.

Sierwald, P. 2000. Description of the male of *Sosippus placidus*, with notes on the subfamily Sosippinae (Araneae, Lycosidae). Journal of Arachnology 28: 133–140.

Silva Davila, D. 2003. Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). Bulletin of the American Museum of Natural History 274: 1–86.

Simon, E. 1886. Etudes arachnologiques. 18e mémoire. XXVI. Matériaux pour servir à la faune des arachnides du Sénégal (suivi d'une appendice intitulé: Descriptions de plusieurs espèces africaines nouvelles). Annales de la Société Entomologique de France ("1885") 5: 345–396.

Simon, E. 1892. Histoire naturelle des araignées. Vol. 1: 1–256. Paris: Roret.

Simon, E. 1893. Histoire naturelle des araignées. Vol. 1: 257–488. Paris: Roret.

Simon, E. 1897. Histoire naturelle des araignées, 2nd ed. Paris: Roret.

Spagna, J.C., and R.G. Gillespie. 2008. More data, fewer shifts: molecular insights into the evolution of the spinning apparatus in non-orb-weaving spiders. Molecular Phylogenetics and Evolution 46: 347–368.

Szüts, T., and N. Scharff. 2009. Revision of the living members of the genus *Tomocyrba* Simon, 1900 (Araneae: Salticidae). Contributions to Natural History 12: 1337–1373.

Tietjen, W.J., and J.S. Rovner. 1980. Trail-following behaviour in two species of wolf spiders: sensory and etho-ecological concomitants. Animal Behaviour 28: 735–741.

Tillinghast, E.K., and M.A. Townley. 1994. Silk glands of araneid spiders. Selected morphological and physiological aspects. *In* D. Kaplan, W. Adams, B. Farmer, and C. Viney (editors), Silk polymers: materials science and biotechnology: 29–44. Washington, DC: American Chemistry Society.

Townley, M.A., and E.K. Tillinghast. 2003. On the use of ampullate gland silks by wolf spiders (Araneae, Lycosidae) for attaching the egg sac to the spinnerets and a proposal for defining nubbins and tartipores. Journal of Arachnology 31: 209–245.

Townley, M.A., and E.K. Tillinghast. 2009. Developmental changes in spider spinning fields: a comparison between *Mimetus* and *Araneus* (Araneae: Mimetidae, Araneidae). Biological Journal of the Linnean Society 98: 343–383.

Townsend, V.R., Jr., and B.-E. Felgenhauer. 1998a. Cuticular scales of spiders. Invertebrate Biology 117: 318–330.

Townsend, V.R., Jr., and B.E. Felgenhauer. 1998b. The cuticular scales of lynx spiders (Araneae, Oxyopidae). Journal of Morphology 236: 223–231.

Townsend, V.-R., Jr., and B.-E. Felgenhauer. 1999. Ultrastructure of the cuticular scales of lynx spiders (Araneae, Oxyopidae) and jumping spiders (Araneae, Salticidae). Journal of Morphology 240: 77–92.

Townsend, V.-R., Jr., and B.-E. Felgenhauer. 2001. Phylogenetic significance of the morphology of the cuticular scales of the lynx spiders (Araneae: Oxyopidae). Journal of Zoology 253: 309–332.

Ubick, D., and N.I. Platnick. 1991. On *Hesperocranum*, a new spider genus from western North America (Araneae, Liocranidae). American Museum Novitates 3019: 1–12.

Ubick, D., and R.S. Vetter. 2005. A new species of *Apostenus* from California, with notes on the genus (Araneae, Liocranidae). Journal of Arachnology 33: 63–75.

Uhl, G., S.H. Nessler, and J.M. Schneider. 2010. Securing paternity in spiders? A review on occurrence and effects of mating plugs and male genital mutilation. Genetica 138: 75–104.

Versteirt, V., C. Deeleman-Reinhold, and L. Baert. 2010. Description of new species of the genus *Pteroneta* (Arachnida: Araneae: Clubionidae) from Papua New Guinea. Raffles Bulletin of Zoology 56: 307–315.

Wagner, W.A. 1887. Copulations Organe des Männchens als Criterium für die Systematik der Spinnen. Horae Societatis Entomologicae Rossicae 22: 3–132.

Wanless, F.R. 1978. A revision of the spider genus *Portia* (Araneae: Salticidae). Bulletin of the British Museum of Natural History, Zoology 34: 83–124.

Wanless, F.R. 1979. A revision of the spider genus *Brettus* (Araneae: Salticidae). Bulletin of the British Museum of Natural History, Zoology 35: 127–200.

Wanless, F.R. 1981. A revision of the spider genus *Hispo* (Araneae: Salticidae). Bulletin of the British Museum of Natural History, Zoology 41: 179–198.

Wanless, F.R. 1982. A revision of the spider genus *Cocalodes* with a description of a new related genus (Araneae: Salticidae). Bulletin of the British Museum of Natural History, Zoology 42: 263–298.

Wanless, F.R. 1984. A review of the spider subfamily Spartaeinae nom. n. (Araneae: Salticidae), with descriptions of six new genera. Bulletin of the British Museum of Natural History, Zoology 46: 135–205.

Wanless, F.R. 1985. A revision of the spider genera *Holcolaetis* and *Sonoita* (Araneae: Salticidae). Bulletin of the British Museum of Natural History, Zoology 48: 249–278.

Wanless, F.R. 1987. Notes on spiders of the family Salticidae. 1. The genera *Spartaeus*, *Mintonia* and *Taraxella*. Bulletin of the British Museum of Natural History, Zoology 52: 107–137.

Wiehle, H. 1965. Die *Clubiona* – Arten Deutschlands, ihre natürliche Gruppierung und die Einheitlichkeit im Bau ihrer Vulva. Senkenbergiana Biologica 46: 471–505.

Wiehle, H. 1967. Beiträge zur Kenntnis der deutschen Spinnenfauna, V. (Arach., Araneae). Senckenbergiana Biologica 48: 1–36.

Wiens, J.J. 2001. Character analysis in morphological phylogenetics: problems and solutions. Systematic Biology 50: 689–699.

Wijesinghe, D.P. 1997. Relationships of spartaeine and other primitive jumping spiders, with reviews of *Cyrba* and *Cocalus* and description of a new genus (Arachnida: Araneae: Salticidae). Ph.D. dissertation, City University of New York.

Wood, H.M., C.E. Griswold, and R. Gillespie. 2012. Phylogenetic placement of pelican spiders (Archaeidae, Araneae), with insight into evolution of the "neck" and predatory behaviors of the superfamily Palpimanoidea. Cladistics 28: 598–626.

Wunderlich, J. 2004. The new spider (Araneae) family Borboropactidae from the tropics and fossil in Baltic amber. Beiträge zur Araneology 3: 1737–1746.

Yu, L., and J.A. Coddington. 1990. Ontogenetic changes in the spinning fields of *Nuctenea cornuta* and *Neoscona theisi* (Araneae, Araneidae). Journal of Arachnology 18: 331–345.

Zhu Ming, S., G. Tang, F. Zhang, and X. Song Da. 2006. Revision of the spider family Trochanteriidae from China (Araneae: Gnaphosoidea). Zootaxa 1140: 31–51.

APPENDIX 1

MATERIAL EXAMINED

Species, authors, and voucher data examined for this study. Species marked with (*) are scored in final dataset. Institutional acronyms are detailed in the acknowledgments section.

Acanthoctenus cf. *spinipes** (Ctenidae). PERU: Loreto: Río Samiria, 0442S 7418W, fogging 7h.8c 8t'.8o 8e', 1♂ 1♀ (CAS), V.1990, T. Edwin et al., 2♂ 1♀ (MUSM, in AMNH; voucher D. Silva Dávila study 2000, SEM D. Silva Dávila VIII.2000; SEM preparations MJR-613–616). MEXICO: San Luis Potosí: 1 mi SW Tamazunchale, 21°15′N 94°49′W, 25.VII.1966, J. and W. Ivie, 1 male 3 immatures

(AMNH, identified by D. Silva Dávila, 1996; tapetum observed). OTHER SOURCES: Silva Davila (2003), Griswold et al. (2005).

Acanthoctenus sp. (Ctenidae). ARGENTINA: Jujuy: P. Nac. Calilegua, Seccional Aguas Negras, 23° 45′ 43.3″ S, 64° 51′ 04.7″ W, (+/− 10 m, WGS84), elev. 605 m (GPS), col. C. Grismado, M. Izquierdo, F. Labarque, G. Rubio, M. Burger, P. Michalik, P. Carrera, A. Ojanguren, C. Mattoni, 06–11.XII.2008, night manual collection, 1♂ (MACN-Ar, temporary preparation MJR-1318, freshly killed, tapetum visible).

*Aglaoctenus lagotis** (Holmberg) (Lycosidae). ARGENTINA: Entre Ríos: P. Nac. El Palmar, camino al Mirador, 22–23.XI.2003, C. Grismado, A. Ojanguren, F. Labarque, 1♀ (MACN; SEM preparations MJR-1019, 1020, 1023); 16–18.VIII.2003, A. Ojanguren, L. Piacentini, F. Labarque, 1♂ (MACN; SEM preparations MJR-1021, 1022). OTHER SOURCES: Santos and Brescovit (2001).

*Agroeca brunnea** (Blackwall) ("Liocranidae"). BELGIUM: Ferrières, Station III, 22.IV–4.XI.1983, L. Baert, J. Kekenbosch, R. Detry, 5♂ 2♀ (IRSN IG 26633; SEM preparations MJR-638–642; respiratory system examined); Chokier (Carr. Sacré), MOMR FS 70 st. II, 3.V.1991–21.IV.1992, R. Detry, several ♂ and ♀ (IRSN IG 27748). All identified by J. Kekenbosch.

Alcimochthes limbatus Simon (Thomisidae). SINGAPORE: Main Island, Lim Chu Kang mangroves, N 1.44° E 103.70°, W. Maddison, I. Agnarsson, J.X. Zhang, 13.V.2005, beating vegetation or on foliage, 1♀, det. C.J. Grismado 2006 (AMNH-UBC/MACN-Ar to be distributed; temporary preparations PMF-245, CJG-588).

*Amaurobioides africana** Hewitt (Anyphaenidae). NAMIBIA: Luderitzbucht, intertidal rocks (26°35′S, 15°10′E), 8–10.X.1984, C. Griswold and T. Meikle Griswold, 1♂ 3♀ 2 immatures (CAS). SOUTH AFRICA: Western Cape: Kommetjie, 34°9′S 18°20′E, 30 air km S of Cape Town, intertidial zone, under rocks, 13.III.2001, L. Prendini, D. Ubick, 1♀ (CAS; SEM preparations MJR-272, 273), 2♀, 4 immatures (CAS).

Amaurobius similis (Blackwall) (Amaurobiidae). DENMARK: Zealand, Gentofte, 55°44.47N 12°32.99E, 15.X.2002, N. Scharff, 1♂ (ZMUC, voucher for AMNH cryocollection 110622; temporary mount MJR-872 for tapeta symmetry axes: ALE oblique externally down, PME longitudinal, PLE horizontal).

*Ammoxenus amphalodes** Dippenaar and Meyer (Ammoxenidae): SOUTH AFRICA: Free State: Deelhoek, 28°54′S 26°07′E, 4.VI.2000, C. Haddad, 2♂ 3♀; 1♂ 1♀ (SEM preparations MJR-873–875).

*Ammoxenus coccineus** Simon (Ammoxenidae): SOUTH AFRICA: 50 km E Gobabeb, 27.II–27.III.1979, B. Wharton, 2♂ 2♀ (AMNH, identified by N. Platnick, 1989). Windhoek District, Gocheganas 26, SE2217 Cc, pres. pitfall traps, 22.I–22.II.1982, M.L. Penrith, 1♀ (AMNH, identified by Tharina Bird, 2002, after SEM images of ♀ genitalia; SEM preparations MJR-596–599, 844); Okondeka, 18°57′S 15°50′E, pres. pitfall traps, 12.II–16.III.1987, E. Griffin, 1♀ (AMNH); Garib Ost 275, SE 237 Ba, pres. pitfall traps, 13–20.XII.1988, E. Griffin, 1♀ (AMNH).

*Anagraphis pallens** Simon (Gnaphosidae). ISRAEL: Hatira ridge, Southern Israel, 8.V.1991, pitfall trap, Y. Lubin, (AMNH; SEM preparations MJR-318–321); 6.IV.1991, pitfall trap, Y. Lubin, (AMNH; SEM preparation MJR-322). All identified by G. Levy. OTHER SOURCES: Levy (1999).

*Anyphaena accentuata** (Walckenaer) (Anyphaenidae). POLAND: Chojnów, woj. Warszawskie, 7.VI.1987, B. and M. Malkin, 2♀ (AMNH; SEM preparations MJR-292–296); same data, 13.VI.1967, 1♂ (AMNH); Kazimierz Dolny, 15–21.V.1987, B. and M. Malkin, 1♂ (AMNH; SEM preparations MJR-297, 298). OTHER SOURCES: Huber (1995b), Brescovit (1997).

Anyphops sp.* (Selenopidae). SOUTH AFRICA: E. Transvaal, 11 km SE Pilmgrins Rest., 1400 m, relict native forest, FITs, #85-275, 11–31.XII.1985, S. and J. Peck, 2♂ 2♀ 2 immatures (AMNH; SEM preparations MJR-913–914, 955–957, eyes dissected, respiratory system from immature).

*Aphantochilus rogersi** O. P.-Cambridge (Thomisidae). ARGENTINA: Misiones: El Dorado, 26°28′S 54°43′W, 1.IX–15.XI.1964, A. Kovacs, 1♀ (AMNH; SEM preparations MJR-191, 192, 204); P. Nac. Iguazú, II.1985, M.J. Ramírez 4♂ (MACN-Ar; temporary preparations PMF-167, ARAMR000780). Santa Fe: Las Gamas, 20 km W Vera, 27–30.X.1994, M.J. Ramírez & J. Faivovich, 2♀ (MACN-Ar; temporary preparations PMF-169–171, ARAMR000781). BRAZIL: Matto Grosso: Vila Vera, 12°46′S 55°30′W, X.1973, M. Alvarenga, 1♂ (AMNH; SEM preparation MJR-865). PARAGUAY: Apa, I–II.1909, 1♂ 1♀, 1♂ and 1♀ penultimates, 1 immature (AMMH; SEM preparation MJR-866).

*Apodrassodes quilpuensis** (Gnaphosidae). CHILE: Aconcagua: Juncal, 1950 m, 5.I.1984, P. Goloboff 1♂ 1♀ (MACN-Ar; SEM preparations MJR-1165–1175). Quillota: P. Nac. La Campana, Palma de Ocoa, 500 m, S32° 56′ 33.4″ W71° 05′ 02.1″, 17 Feb 2005, M. Ramírez & F. Labarque 1♂ (MACN-Ar; tapeta visible; ARAMR000221; Palma de Ocoa 17 FML/1). Santiago: El Canelo, X.1963, Fritz, 1♀ (MACN).

*Apostenus californicus** Ubick and Vetter (Liocranidae). USA: California: San Diego Co., Julian, 4839 Pine Ridge Ave., 4275 ft, 35°02′34″N

116°37′49″W, in *Quercus kelligi* and *Q.* sp. oak duff, 31.III.2002, R. Vetter, 1♂ 1♀ (AMNH, boiled, SEM preparations MJR-832–834, 915). OTHER SOURCES: SEM images and drawings by D. Ubick (in litt.), Ubick and Platnick (2008).

*Araneus diadematus** Clerck (Araneidae). CANADA: Ontario: Swansea, W of High Park, 43°41′N 79°28′W, 1.IX.1945, W. Ivie and T. Kurata, 1♂ 4♀ (AMNH; SEM preparations MJR-819–822). OTHER SOURCES: Scharff and Coddington (1997), Nikolaj Scharff (in litt., images of tapeta).

Araneus sp. (Araneidae). USA: New York: Long Island, Centereach, 184 Mark Tree Road, 17.X.2002, V. Ovtsharenko, 1♀ (MACN-Ar; SEM preparation MJR-855).

*Ariadna boesenbergi** Keyserling (Segestriidae). ARGENTINA: Buenos Aires: Sierras de Olavarría, 3–6.XII.1992, M. Ramírez, 4♀ (MACN-Ar 10201; SEM preparations MJR-934–936); Sarandí, in bathroom, I.1998, C. Grismado, 1 male (MACN-Ar 10242; SEM preparation MJR-933).

*Austrachelas pondoensis** Haddad et al. (Gallieniellidae). SOUTH AFRICA: Eastern Cape: Lusikisiki district, Mzimhlava river mouth, 31°20′S, 29°40′E, I.1980, M.E. Baddeley (coastal evergreen forest), 12♀ 1♂ (MRAC 159047, SEM preparations MJR-1031–1038, 1063–1065, temporary mount CJG-154); I.1980, 1♂ (MRAC 166821, SEM preparations MJR-1039, 1040, temporary mounts CJG-155, 156).

Austrochilus forsteri Grismado et al., 2004 (Austrochilidae). CHILE: Malleco: Monumento Natural Contulmo, elev. 340m, 38°01′S, 73°11′W, 19–21.XII.1998, M. Ramírez, L. Compagnucci, C. Grismado, L. Lopardo, early spiderlings, stage with most hairs (MACN-Ar; SEM preparation MJR-17, fixed 9.I.1999; SEM preparation MJR-67, fixed 29.XII.1998, just molted); same data, early spiderlings, stage with few hairs (MACN-Ar; SEM preparations MJR-24, 25, fixed 25.XII. 1998).

Austrochilus franckei Platnick (Austrochilidae). CHILE: Concepción: 8 km W Florida, 220 m, xerophytic forest, 36°49′S 72°44′W, 10.I.1995, N. Platnick, K. Catley, D. Silva Dávila, 2♂ 1♀ (AMNH; sperm duct and bulb tendons observed).

*Badumna longinqua** (C.L. Koch) (Desidae). NEW ZEALAND: Ship Cr. (bch.) B of Haast, 8.XII.1977, E.I. Schlinger, 1♂ 1 immature (CAS). USA: California: San Mateo Co., Pacifica, 13.V.1995, K. Ribardo, 2♀ 1♀ subadult, (CAS). OTHER SOURCES: Forster (1970b), Griswold et al. (2005).

Boliscus cf. *tuberculatus** (Thomisidae). THAILAND: Nakhon Si Thammarat Prov., Khao Luang NP, 8°43′25.2″N 99°40′7.7″E, 355 m, 10–12.X.2003, ATOL Expedition 2003, 2♂ 1♀ penultimate (MACN-Ar to be distributed; SEM preparations MJR-1274–1281, CJG-323–325, ARAMR000328, 329).

*Borboropactus bituberculatus** Simon (Thomisidae). VIETNAM: Ha Tinh: HuongSon District, An River, HuongSon Forest, 13 Km W Rt. 8, ca.18°20′52″N, 105°14′41″E, (ref. HS24) 680 m, mammalogist's pitfalls, v.17.1998, D. Silva Dávila 5♂ 1♀ (AMNH/IEBR; SEM preparations MJR-103–104, 111–113, 158, 170, respiratory system examined); entomologist's pitfalls, 1♂ (AMNH/IEBR, temporary mounts PMF-190–191, ARAMR000791); 230 m, tree bark, 2♂ (AMNH/IEBR, temporary mounts CJG-502, ARAMR000933); 230 m, tree bark, 1♀ (AMNH/IEBR, temporary mounts, CJG-501, ARAMR000932). THAILAND: Nakhon Si Thammarat: Khao Luang NP, N8°43′25,2″ E99°40′7,7″, 355 m, 10–12.X.2003, ATOL Expedition 2003 (ZMUC; temporary mounts PMF-192–194, ARAMR000132).

Brachyphaea cf. *simoni** ("Corinnidae" incertae sedis). KENYA: 12 mi E Narok, 31.XII.1959, E. Ross, 1♂ 1♀ (CAS; SEM preparations MJR-357–363); 15 mi SW Nairobi, 5400′, 15.I.1970, M.E. Irwin and E.S. Ross, 2♀ (CAS); Rift Valley: Lake Naivasha, Fishermans's Camp, (ca. 0°45′S 36°20′E, 19.X.1992, V. and B. Roth, 1♂ (CAS). TANZANIA: 24 mi S Namanga, 1300 m, 20.X.1957, E.S. Ross and R.E. Looch, 1 male 1♀ (CAS; respiratory system from male).

*Calacadia dentifera** (Amphinectidae: Metaltellinae). CHILE: Osorno: P. Nac. Puyehue: Aguas Calientes, 13–17.XII.1998, M. Ramírez, L. Compagnucci, C. Grismado, L. Lopardo, 3♀ (MACN). ARGENTINA: Neuquén: P. Nac. Lanín, Lago Queñi, 15.II.1996, M. Ramírez, 3 males 1♀ (MACN; SEM preparation MJR-966). Identified by C. Grismado, 2003.

Calamoneta sp. (Eutichuridae). AUSTRALIA: Queensland: 60 km NE Dalby, 900 m, Bunya Mountains, FIT Araucaria forest, 17.VI–19.VIII.1982, S. and J. Peck, 1♀ 9 juv. (AMNH; respiratory system examined from immature, temporary mount MJR-942). NOTES: Four simple tracheae, the medians very long, apparently curved backwards at anterior border of abdomen. No epigastric tracheae.

*Camillina calel** (Gnaphosidae). ARGENTINA: Mendoza: San Carlos: Arroyo El Carrizalito, 23.I.1979, A. Roig, 1♀ (MACN-Ar; temporary mount CJG-395; ARAMR000864). Salta: Ruta Nac. 40 (N), ca. Palo Pintado, 4.XI.2004, C.J. Grismado, L.A. Compagnucci, 1♂ (MACN-Ar; temporary mounts CJG-396, PMF-129, 130; ARAMR000767). Tolombón, Ruta Nac. 40 (N) Km 1038, bajo troncos y piedras, 2.XI.2004, C. Grismado, L. Compagnucci 1♀ 1 juv. (MACN-Ar; SEM preparations MJR-1176–

1182). Arroyo El Molle, entre Cachi y Payogasta, bajo piedras, 4.XI.2004, C. Grismado, L. Compagnucci 1♂ 1♀ (MACN-Ar; SEM preparations MJR-1183–1186).

*Castianeira trilineata** (Hentz) (Corinninae: Castianeirinae). OHIO: Franklin Co.: Sharon Woods Metropolitan Park, 0.8 km S Park Rd. entrance, pitfall, sta. 17, 31.VII–7.VIII.1973, A. Penniman, 1♀ (AMNH; SEM preparations MJR-545–549); pitfall, sta. 21, 26.V–5.VI.1973, A. Penniman, 1♂ (AMNH; SEM preparations MJR-550, 551); pitfall, sta. 20, 10–17.VII.1973, A. Penniman, 2♂ (AMNH; base of tracheae examined; temporary preparation MJR-1359); pitfall, sta. 15, 3–10.VII.1973, A. Penniman, 1♀ (AMNH). All identified by A. Pennimann, VIII.1974.

*Cebrenninus rugosus** Simon (Thomisidae). PHILIPPINES: Laguna: 4 km SE Los Banos, Makiling: berlese debris under bark, 9.IV.1977, L. Watrous AL-1855, 1♀ 1 immature (AMNH; SEM preparations MJR-165–168); Luzon, Laguna Prov. Mt Maquiling, 3000–3700 ft, 18.XI.1945, B. Malkin 1♂ (AMNH; SEM preparations MJR-173, 180); same data, 1100–1400 ft, 29.IX.1945, B. Malkin and Jewett, Jr., 1♂ 1♀ (AMNH). VIETNAM: Tuyen Quang Prov.: NaHang Reserve, 360 m, FIT, 16–20.V.1997, S. Peck 97-10, (AMNH; tapeta preparation MJR-864). THAILAND: Surat Thani: Khao Sok NP, Wing Hin Waterfall trail, N 8°55′0.4″ E 98°31′40.9″, 19–20.X.2003, 300 m, 1♂ (MACN-Ar 10456, temporary mount CJG-254, ARAMR000042). MALAYSIA: Selangor: Canyon near Ulu Gombak, N3,325° E101,765°, 15.V.2005, 275 m, W. Maddison, D. Li, I. Agnarsson, J.X. Zhang, 1♂ (UBC, WPM#05-027, temporary mount PMF-99). Pahang: Genting Highlands, N3,400° E101,777°, 15–16.V.2005, 1000 m, W. Maddison, D. Li, I. Agnarsson, J.X. Zhang, 1♀ (UBC, WPM#05-023, temporary mounts PMF-96–98, ARAMR000391).

*Centrothele mutica** (Simon) (Lamponidae). AUSTRALIA: Queensland: Burleight Headland, 28°10′S, 153°33′E, rainforest pitfall, 25.V–13.X.1975, G.S. Monteith, 1♀ (QMB S26850; SEM preparations MJR-606–608); Mount Glorious, 27°20′S 152°46′E, in house, 10.V.1988, K. Hiller, 1♂ (QMB S6302). OTHER SOURCES: Platnick (2000).

Cf. Eutichuridae QLD* (Eutichuridae). AUSTRALIA: Queensland: 20 km SW Mossman, 900 m, Mt. Lewis, FIT, rainforest, 26.VI–1.VIII.1982, S. & J. Peck, 1♀ (AMNH; SEM preparations MJR-947, 948, temporary preparation MJR-938); 10 km SE El Arish, Laceys Creek nr. Mission Beach, 40 m, FIT, rainforest, 23.VI–5.VIII.1982, S. & J. Peck, 3 males 2 immatures (AMNH; SEM preparations MJR-949–952, temporary preparations MJR-937, 1356).

Cf. Gnaphosoidea TEX* (uncertain family, OMT clade). USA: Texas: Presidio Co., Ojito Adentro, Big Bend Ranch St. Park, P.W. Hayder, 14.X.2000, AM 1256, 1♀ (AMNH). Brewster Co., Big Bend Ranch State Park: Sandy Canyon, N29°33.30′ W103°47.60′, 1212 m, 22.IX–4.X.2005, N. Horner & G. Broussard, propylene-glycol pitfall trap, 1♀ (AMNH; ARANP000019).

Cf. Liocranidae LIB* (uncertain family, CTC clade). LIBERIA: Bong Range Forest, (06°49N 010° 17W), pitfalls in rain forest, 12.VI.2005, Flomo D., 1♀ (MRAC 216964; SEM preparations MJR-1073–1078); 1♀ (MRAC 216968); 13.III.2005, 1♂ (MRAC 216818); 26.III.2005, 1♂ 1♀ (MRAC 216735; temporary mount MJR-1322); 15.II.2005, 1♂ (MRAC 216840).

Cf. *Medmassa* THA* (Corinnidae). THAILAND: Chiang Mai Prov., Doi Chiang Dao WS, Amphen Chiangdao, Mae Ta Man forest, field station, N 19°19′13.2″; E 98°49′47.0″, 1500 m, 1.X.2003, ATOL Expedition 2003 1♀ with maturity exuvia (MACN-Ar; SEM preparations MJR-1100–1106); 1♀ (MACN-Ar 10443; MJR1.X.2003/1; ARAMR000049).

Cf. *Moreno* ARG.* (Prodidomidae). ARGENTINA: Misiones: Iguazú, 23–26.X.1995, M. Ramírez, (MACN-Ar; SEM preparations MJR-132–137). OTHER SOURCES: Platnick et al. (2005: figs. 9, 10).

Cf. *Patu* sp. (Symphytognathidae). MADAGASCAR: Antsiranana: Nosy Be, P. Nat. de Lokobe, 4.95 km 125° ESE Hellville, S13°24′56.0″ E48°18′27.3″, 13–16.II.2003, 0–200 m, lowland rainforest, D. Andriamalala, C. Griswold, H. Ratsirarson, D. Silva Dávila General collecting day BLF 7999, 6♂ 31♀ 5 immatures (CAS; SEM preparations FML-363–371, temporary preparations CJG-413, 414; ARAMR000878).

Cheiracanthium inclusum (Hentz) (Eutichuridae). USA: CA: Contra Costa Co., Canyon, 22.V.1981, D.G. Denning 1♂ 1♀ (AMNH; SEM preparation MJR-9); New Jersey: Lambertville, 74°56′N 40°22′W, VI.1952, W. Ivie, (AMNH).

*Cheiracanthium punctorium** (Villers) (Eutichuridae). FRANCE: Alpes Maritimes, Aspremont, VIII.1948, M. Thomas, 2♂ 1♀ 2 immatures (IRSN IG 16172; SEM preparations MJR-633–637).

Cheiramiona sp.* (Eutichuridae). TANZANIA: Iringa Distr.: Uzungwa Scarp For. Res., 11 km SE Masisiwe, Kihanga Strm. 8°22′5.7″S 35°58′41.6″E, 1800 m, 17–27.V.1997, understory, ZMUC-SI Exp. 1977, 7♂ 3♀ (USNM, Clubionidae sp.1 det. R. Baptista; SEM preparations MJR-88–92). OTHER SOURCES: Lotz and Dippenaar-Schoeman (1999).

Ciniflella sp. ARG* (Tengellidae). ARGENTINA: Misiones: P. Nac. Iguazú, ruta 101 5 Km E Arroyo Yacuí, S25°41′02.3″ W54°11′57.1″, 310 m, 18.V.2005, M. Ramírez, P. Michalik, F. Labarque, 1♀ (MACN-Ar 10810; SEM preparations MJR-1122–1127; temporary mounts MJR-1121, 1149); 1♂ (MACN-Ar; temporary mount CJG-634; ARAMR000978); area of Garganta del Diablo, S25°42′16.7″ W54°26′28.2″, 250 m, 16–20.V.2005, M. Ramírez, P. Michalik, F. Labarque, 1♂ (MACN-Ar 11314; SEM preparations MJR-1118, 1119); 1♂ (MACN-Ar; temporary mounts CJG-635–637; ARAMR000979).

Ciniflella sp.* BRA (Tengellidae). BRAZIL: Minas Gerais: Lavras, soil, 2002, no collector, 1 male 1♀ (IBSP 39615; SEM preparations MJR-979–986).

*Cithaeron delimbatus** Strand (Cithaeronidae). ETHIOPIA: Awash Nat. Park, Karamara Hotel, 1000 m, under heap of grass, 27.IV.1984, A. Russell-Smith, 2♀ (AMNH; SEM preparations MJR-600–603, 770); nr. Harbona, E Nazret, 1300 m, under stones in *Acacia commiphora* bushland, 9.IV.1986, A. Russell-Smith, 1♂ 1♀ 3 juv. (AMNH; SEM preparation MJR-604). Other sources: Morphology and biology in Platnick (1991c).

Clubiona cf. *maritima* (Clubionidae). MEXICO: Veracruz: Coatzacoalcos (west side), 18°09′N 94°26′W, 11.VIII.1966, J. and W. Ivie, 1♂ (AMNH; SEM preparation MJR-526).

*Clubiona pallidula** (Clerck) (Clubionidae). BELGIUM: Antheit (Corphalie), MOM FS 50 P.M. 23.III.1989–12.IV.1990, R, Detry, 4♂ 4♀ (IRSN IG 29594; SEM preparations MJR-691–695); Koksyde, 1–8.VII.1983, A. Muylaert, 1♂ (IRSN; SEM preparations MJR-696–697). Other sources: Genitalia in Whiele (1965: figs. 38–43), and Huber (1995b).

Cocalodes innotabilis Wanless (Salticidae). PAPUA NEW GUINEA: Kiriwina Is., 14.X.1943, W.B. Jones #24, 1♂ (AMNH; SEM preparations MJR-446, 447).

*Cocalodes longicornis** Wanless (Salticidae). PAPUA NEW GUINEA: Kiriwina Is., 14.X.1943, W.B. Jones #24, 1♀ (AMNH; SEM preparations MJR-442–445); same data, 1♂ (AMNH; SEM preparations MJR-446, 447). Other sources: Wanless (1982).

Cocalodes papuans Simon (Salticidae). PAPUA NEW GUINEA: Hollandia, 250 ft., rain forest, XII.1944, H. Hoogntraol, 1♀ (AMNH; respiratory system examined).

Cocalodes thoracicus Szombathy (Salticidae). PAPUA NEW GUINEA: Hollandia, 14.V.1945, B. Malkin, 1♂ (AMNH, identified by Wanless, 1981; sperm duct examined).

*Copa flavoplumosa** Simon (Corinninae: Castianeirinae). ZIMBAWE: Batoca Gorge & Dibu Dibu River, 17°58′S, 25°57′E, 27–28.X.1990, V.D. & B. Roth, 14♂ 5♀ (CAS; SEM preparations MJR-373–379, respiratory system examined); identified by Charles Haddad (in litt.) from images.

Copa sp. (Corinnidae: Castianeirinae). MADAGASCAR: Toamasina: Res. Analamazaotra, P. Nat. Andasibe, 23 road km E Moramanga, 18°56′38″S, 48°25′03″E, C. Griswold, D. Silva Dávila, D. Andriamalala, 16–18.1.2003, 960 m, rain forest, general collecting, night, BLF7992–994, ♀ ♂ (CAS; ARAMR000144, 145, temporary preparations CJG-192–195).

Copa sp. (Corinnidae: Castianeirinae). KENYA: Shimba Hills National Park, campsite #1, 7–10.VI.1975, A.J. Penniman and B.D. Valentine, 1♀ (AMNH; tapetum observed).

*Corinna bulbula** F.O. Pickard-Cambridge (Corinnidae: Corinninae) (identified by A. Bonaldo from photographs). COSTA RICA: Prov. Alajuela: A.C.A., San Carlos, Reserva Forestal Arenal, Sendero Pilón, 600 m, 17–18.V.1999, G. Carballo col., Malaise L_N_269100_457900 #53363 1♀ (INBIO; SEM preparations MJR-703–707); Prov. Puntarenas: A.C.O., Golfito, P. Natl. Corcovado, Estación Agujas, Cerro Rincón, 745 m, 15.VII—15.VIII.1999, J. Azofeifa col., Malaise L_S_276900 521500 #53001, 1♂ (INBIO; SEM preparations MJR-798, 709); Río Rincón, ACOSA, 200 m, LN_279500_518200, Malaise, 5–7.V.1995, E. Flores, A. Picado, #4520, 1♂ (INBIO). Prov. Guanacaste: Est. Pitilla, Sendero Nacho, 700 m, L N 330200_380200 V.1994, P. Rios, Malaise, #3339, 1♂ 1♀ (INBIO). Other sources: Bonaldo (2000), from *Corinna ducke.*

Crassanapis chilensis Platnick and Forster (Anapidae): CHILE: Osorno: P. Nac. Puyehue: Aguas Calientes, 13–17.XII.1998, M. Ramírez, L. Compagnucci, C. Grismado, L. Lopardo, Moczarski-Tullgren extractor, ♂♀ (MACN-Ar; SEM preparation MJR-677). Other sources: SEM images by Lara Lopardo.

*Creugas gulosus** Thorell (Corinnidae: Corinninae). MEXICO: Nayarit: San Blas, 25–29.VI.1956, W. McDonald, (AMNH; SEM preparations MJR-255, 256). San Luis Potosí: Cueva Chica, 24.V.1974, C. Soliau, 1♂ (AMNH; SEM preparation MJR-257); Cueva Chica, 2.IV.1942, 1♂ 1♀ (AMNH; SEM preparations MJR-258, 259). Guerrero: Grutas de Juxtaphuaca, 4 mi N Colotlipa, 15.VIII.1966, F. Fish, J. and J. Reddell, 1♀ (AMNH; SEM preparation 857). Other sources: Bonaldo (2000).

Cryptothele alluaudi Simon (Zodariidae). Seychelles, Mahé Centre, Morne Blanc, 667 m, 24–25.VII.1972, P.L. Benoit, J.J. Van Mol, 7 immatures (MRAC 143.081; identified by P.L. Benoit 1974, SEM preparations MJR-299–302). Other sources: Benoit (1978).

Cryptothele sp. (Zodariidae). MYANMAR: Mandalay Division: Mt. Popa Wildlife Reservation, near resort, 2.15 km 136° ESE PoPaMyo, N20°55′7.0″, E95°13′14.9″, D. Ubick and C. Griswold, 23.IX.2003, El 2100 deciduous forest, along roadcut at night, 1 male (CAS; temporary mounts CJG-198, 199, 594; ARAMR000147); Magway Division: Shwe Settaw Wildlife Reservation, N20°5′51.1″, E94°33′24.5″, C. Griswold, 28–29.IX.2003, deciduous forest, general collecting, 1♀ (CAS; temporary mounts CJG-196, 197; ARAMR000146). SRI LANKA: "Ceylon, 1968, Hung. Soll. Zool. Exp. B 65," 1♀ (in AMNH; SEM preparations MJR-732, 733).

Ctenus cf. *crulsi** (Ctenidae). PERU: Madre de Dios: 15 km E Puerto Maldonado, 1233S, 6903W 200 m, 15–17.VIII.1989, D. Silva Dávila, 2♂ 2♀ (MUSM; SEM preparations MJR-609–612; also SEM by D. Silva Dávila Jan. 1999, male abdomen and I left metatarsus); 15–17.VIII.1989, D. Silva Dávila, several ♂ ♀ and immatures, (MUSM; SEM by D. Silva Dávila Jan. 1999, legs, spinnerets, carapace, spermathecae). All identified by D. Silva Dávila. OTHER SOURCES: Silva Davila (2003).

Cybaeodamus taim Lise, Ott and Rodrigues (Zodariidae). ARGENTINA: Mendoza: Puente del Inca, 23.III.1976, A. Roig, 7♂ 9♀ 5 immatures (MACN-Ar; identified by C. Grismado, 2011, SEM preparations MJR-670–674).

*Cycloctenus nelsonensis** Forster (Cycloctenidae). NEW ZEALAND: South Isle: #30, Neslon, Mangarakau Scenic Reserve, 17–18.III.1995, J. Boutin, Savary, 1♂ 4♀ (CAS, identified by J. Boutin, 1995, who compared with type; SEM preparations MJR-617, 618, 715, 716). OTHER SOURCES: Forster (1979), Silva Davila (2003).

Cyrioctea aschaensis Schiapelli and Gerschman (Zodariidae). ARGENTINA: Catamarca: Singuil, 19–21.I.1987. P. Goloboff, C. Szumik, 6♀ 2 immatures (MACN-Ar; SEM preparations MJR-667–669). OTHER SOURCES: Platnick (1986).

Cyrioctea calderoni Platnick (Zodariidae). CHILE: Región V (Valparaíso): Quillota: Palmas de Ocoa, P. Nac. La Campana, burned site, 21.VI.1985, pitfall #6, R. Calderón G. 1♂ (AMNH, identified by N. Platnick, 1986; SEM preparation MJR-282). OTHER SOURCES: Platnick (1989).

Cyrioctea spinifera Simon (Zodariidae). CHILE: Choapa: 6.5 km N Los Vilos, 10 m, dunes, 16.X.1992, N. Platnick, P. Goloboff, K. Catley, 2♂ 13♀ 11 immatures (AMNH, identified by N. Platnick, 1993).

Desis formidabilis (O. P.-Cambridge) (Desidae). SOUTH AFRICA: Western Cape: "The Island," Kommetje, Cape Peninsula, V.1966, B. Lamoral, 3♀ 1♂ (CAS, identified by Lamoral; SEM preparation MJR-274); Kommetjie, 34°9′S 18°20′E, 30 air km S of Cape Town, intertidial zone, under rocks, 13.III.2001, K. Muller, C. Prinsloo, Prendini, D. and S. Ubick, ♀ ♂ (CAS, identified by D. Ubick, 2001; SEM preparations MJR-275–280). OTHER SOURCES: Forster (1970b).

*Desognaphosa yabbra** Platnick (Trochanteriidae). AUSTRALIA: New South Wales: Gibbergunyah Range Rd., 150 m W Rocky Creek crossing, Whian Whian SF, Big Scrub Flora Reserve, 180 m, 4.II–9.IV.1993, 28°38′S, 153°19′E, M. Gray, G. Cassis, 1♀ several males (AMS KS35793; SEM preparations MJR-594–595, respiratory system examined from male). Queensland: Binna Burra, Lamington N. Park, S28°11′55.4″, E153°11′14.8″, elev. 800 m, 21–23.III.2006, M. Ramírez, R. Raven, B. Baehr, C. Griswold, D. Silva Dávila, rainforest 1♀ (MACN-Ar 11108); same data, 1♀ (MACN-Ar 11556). OTHER SOURCES: Spinnerets from Platnick (2002: figs. 181–186).

*Dictyna arundinacea** Linnaeus (Dictynidae). SCOTLAND: Skibo Castle, Dornoch, Sutherland, August, 1935, R. Miller, 9♀ (AMNH, identified by W. Gertsch; SEM preparation MJR-818). FINLAND: Helsingors, Haga, 3.VI.1951, W. Hackman, 2♂ 1♀ (AMNH). OTHER SOURCES: Lehtinen (1967), Griswold et al. (2005).

*Doliomalus cimicoides** (Nicolet) (Trochanteriidae). CHILE: Reg. V: Quillota: PN La Campana, Palma de Ocoa, 770 m, S32° 57′ 40.4″ W71° 03′ 34.0″, 18 Feb 2005, M. Ramírez & F. Labarque 1♀ (MACN-Ar; SEM preparations MJR-1230–1236, temporary mount MJR-1237); 1♀ (MACN-Ar; ARAMR000225). Santiago: El Canelo, X.1963, Fritz, 4 immatures (MACN-Ar; tracheae and tapetum examined). ARGENTINA: Neuquén: Pucará, I–II.1971, A. Schajovskoy, 1♂ (MACN-Ar; SEM preparations MJR-1238–1240).

*Dolomedes tenebrosus** Hentz (Pisauridae). USA: Pennsylvania: NE Jamison (Horseshoe Bend, Neshaminy Cr.), 40°16′N 75°03′W, VII.1955, W. Ivie, several ♀ (AMNH, identified by Carico, 1981; SEM preparations MJR-516–520). OTHER SOURCES: Sierwald (1989, 1990), Griswold (1993), Silva Davila (2003).

Donuea sp.* ("Liocranidae"). MADAGASCAR: Fianarantsoa: P. Nat. Ranomafana: Vohiparara, Piste Touristique, 21°13.6′S, 47°24.0′E, ca. 100 m, 19.IV.1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, E. Rajeriarison, J. Ranoriaranarisoa, J. Schweikert, D. Ubick, 1♀ 2 immatures (CAS; SEM preparations MJR-310–315); P. Nat. Ranomafana: Talatakely 21°14.9′S, 47°25.6′E, 19–30.IV.1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, J. Ranoriaranarisoa, J. Schweikert, D. Ubick, 1♂ 2 immatures (CAS; SEM preparations MJR-316, 317); P. Nat. Ranomafana: 2.3 km N Vohiparara village, 21°12.8′S 47°23.0E, ca 1100 m, 24–25.IV.1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, E.

Rajeriarison, J. Ranoriaranarisoa, J. Schweikert, D. Ubick, 1♂ (CAS).

Dorymetaecus spinnipes Rainbow (Phrurolithidae). LORD HOWE ISLAND: Lord Howe Island Area, XII.1915–I.1916, A.M. Lea, ♀ holotype (South Australian Museum NN275, old registration N1981336, ex Entomology Insect Reg. I11535, on Kentia Palm, examined).

*Drassinella gertschi** Platnick and Ubick (Phrurolithidae). USA: California: San Diego Co., San Diego Springs, 28.III.1960, W. Gertsch, W. Ivie and Schrammel 1♂ 1♀ 2 immatures (AMNH; SEM preparations MJR-244–247, posterior respiratory system examined from immature); Baja California: 40 mi S Tecate, 29.IV.1961, W. Gertsch and V. Roth, 1♂ 1 immature (AMNH; SEM preparations MJR-248–249). OTHER SOURCES: Platnick and Ubick (1989).

Eilica amambay Platnick (Gnaphosidae). ARGENTINA: Misiones: Pto. Libertad, X.1953, Schiapelli, Di Pere, 2♀ (MACN-Ar 5945; temporary mounts CJG-475, PMF-136–138; ARAMR 000917, ARAMR000771). Santiago del Estero: P. Nac. Copo, S26°04′ W61°44′, pitfalls, 23–25.X.2003, F. Cuezzo, 2♂ (MACN-Ar; SEM preparations MJR-1154–1156, 1164; temporary mounts PMF-134, 135, CJG-490; ARAMR 000770).

Eilica cf. *trilineata** (Gnaphosidae). ARGENTINA: Santiago del Estero: P. Nac. Copo, área de pobladores, 22–24.II.2004, col. C. Grismado, A. Ojanguren, F. Labarque, L. Compagnucci 1♂ (MACN-Ar; SEM preparations MJR-1157–1163).

Elassoctenus sp. (Miturgidae). AUSTRALIA: Queensland: Binna Burra, Lamington N. Park, S28°11′55.4″ E153°11′14.8″, M. Ramírez, R. Raven, B. Baehr, C. Griswold, D. Silva Dávila, 21–23.III.2006, 800 m, rainforest, 1 male (MACN-Ar 11103; temporary preparations 156, 157; ARAMR000682); same data, 1♀ (MACN-Ar 11100; temporary preparation PMF-146). Identified by R. Raven 2006, from images, in litt.

Elaver cf. *tigrinella** (Clubionidae). COSTA RICA: Monteverde, Puntarenas, 1.XII.1960, C.W. Palmer, 1♂ (AMNH; SEM preparations MJR-527, 528); 1♀ (AMNH; SEM preparations MJR-532–536); Prov. Guanacaste, Est. Pitilla, Sendero Nacho. 700 m, May 1994, P. Rios, Malaise, L N 330200_380200 #3339, 1♂ 1♀ (INBIO; somatic morphology scored from these). MEXICO: Hidalgo: Jacala, 21°01′N 99°12′W, 20.IV.1963, W. Gertsch and W. Ivie, 1♀ (AMNH; SEM preparations MJR-529, 530). PANAMA: Chiriqui: Boquete, I.1940, W.C. Wood, 1♂ (AMNH; SEM preparation 531).

*Epidius parvati** Benjamin (Thomisidae). SRI-LANKA: Bellanwila-Attidiya, 24.II.1998, leg. PB KMA, Thomisidae 130, 1♀ 1 immature (CAS; SEM preparations MJR-211, 212, 221, respiratory system examined from immature); 22.II.1998, leg. Benjamin P., Thomisidae 141/142, (CAS; SEM preparation MJR-213). OTHER SOURCES: Benjamin (2000).

Eresus cf. *kollari** (Eresidae). GREECE: Peloponesus: Camp Dimitri Mitropulos, ab. 10 km W Vitina, Tripolis–Olympia Hwy, 1000–1100 m, 15–18.VI.1981, B. and H. Malkin, 1♀ (AMNH); Mistras, 19.VI.1982, B. and H. Malkin, 1♂ (AMNH; SEM preparations MJR-809, 810). MAROCCO: Igrherm, Anti Atlas, 1600–1700 m, 23–29.V.1974, B. Malkin, 1♀ (AMNH; SEM preparations MJR-811, 831). OTHER SOURCES: Schütt (2002), Griswold et al. (2005).

*Eriauchenius workmani** O. P.-Cambridge (Archaeidae). MADAGASCAR: Fianarantsoa: P. Nat. Ranomafana: Talatakely 21°14.9′S, 47°25.6′E, 5–18.IV.1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, J. Ranoriaranarisoa, J. Schweikert, D. Ubick, 3♂ 3♀ and immatures (CAS, SEM preparations MJR-791–797).

Eusparassus cf. *walckenaeri** (Sparassidae). UZBEKISTAN: Surkhandarya Area: Uzun District: foothils on E slopes of Babatag Mountain Range, Dikhana Canyon, ca. 5 Km WSW Akmechet village, 38°01.638′N 68°15.198′E, 722 m, site 14, 20–24.V.2003, L. Prendini & A.V. Gromov, 1♀ 1 penultimate ♀ 1 penultimate ♂ (AMNH; ♀ ARAMR000973 temporary mounts CJG-613–614; tapeta and tracheae observed from penultimate ♂); same data, 1♂ (AMNH; SEM preparations MJR-1194–1198, temporary mount CJG-615; ARAMR 000974); same data, 1♀ (AMNH; SEM preparations MJR-1187–1188); same data, 1♀ (AMNH; SEM preparations MJR-1189–1193).

Eutichuridae MAD* (Eutichuridae?). MADAGASCAR: Fianarantsoa: 7 km W Ranomafana, 900 m, ca. 21.12°S 47.27°E, 1–9.II.1990, W.E. Steiner, 1♀ 2 juv. (USNM); Ranomafana NP, Research Station at Namorona river and surrounding forest, 1000 m, 21°15′S 47°25′E, 21–25.IV.2001, I. Agnarsson & M. Kuntner, 1♂ (USNM, ARAMR000090; SEM preparations MJR-1107–1109); same data, 1♂ (USNM); same data, 1♂ (USNM); same data, 1 juv. 1 subadult male (USNM; KOH digested, tracheae examined, preparation MJR-1357); same data, 1♀ (USNM; ARAMR000953, SEM preparations MJR-1110–1115, temporary mount CJG-570); Ranomafana NP, Vatoharanana camp and surrounding forest, 1200 m, 21°15′S 47°25′E, 23.IV.2001, I. Agnarsson & M. Kuntner, 2♂ (USNM, 1 male ARAMR 000950, temporary mounts CJG-571, 572, 585; 1 male ARAMR000004).

*Eutichurus lizeri** Mello-Leitão (Eutichuridae). ARGENTINA: Jujuy: P. Nac. Calilegua, Mirador, 600 m, for. malaise 87–172, 18–28.XII.1987,

S. and J. Peck, 1♀ (AMNH; SEM preparations MJR-260–262); 22–23.XII.1994, C. Grismado (MACN-Ar; SEM preparations MJR-263, 734). Catamarca: La Viña, 6.II.1986, P. Goloboff, 1♀ (MACN). Córdoba: Salsipuedes, bajo piedras, 7.VIII.1978, P. Goloboff, 1♀ (MACN; respiratory system examined). Buenos Aires: Pergamino, 14.IV.1979, P. Goloboff, 1♂ moulted 14.IV and 17.VI (MACN); 2.VI.1980, P. Goloboff, 1♂ (MACN). OTHER SOURCES: Bonaldo (1994), Silva Davila (2003).

*Falconina gracilis** (Keyserling) (Corinnidae: Corinninae). ARGENTINA: Entre Ríos: P. Nac. El Palmar, 17–18.VIII.2003, A. Ojanguren, L. Piacentini, F. Labarque, 1♂ (MACN-Ar 16703); 11–13.X.2003, C. Grismado, A. Ojanguren, L. Piacentini, F. Labarque, 1♂ (MACN-Ar 16704). Buenos Aires: Campo de Mayo, Km 26 F.C. General Belgrano, en nido de *Annumbius annumbi*, 21.XII.2005, leg. Paola Turienzo, 1♀ (MACN-Ar; SEM preparations MJR-1219–1225. Santiago del Estero: P. Nac. Copo, área de pobladores, 22–24.II.2004, col. C. Grismado, A. Ojanguren, F. Labarque, L. Compagnucci 2♂ (MACN-Ar; SEM preparations MJR-1226–1229); 1♀ (MACN-Ar; temporary mounts CJG-134–135; ARAMR000129); P. Nac. Copo, límite NE, 24–25.II.2004, 1♂ (MACN-Ar; temporary mounts CJG-200, 201, 603; ARAMR000148).

*Filistata insidiatrix** (Forskål) (Filistatidae). ITALY: Siena: 4 km S San Giminiano, Fattoria Voltrona, Reg. Toscania, Italy, 12.VII.2001, M. Ramírez, several ♀ and eggsacs with spiderlings (MACN-Ar; SEM preparations MJR 798–803, 835). SPAIN: Islas Baleares: Mallorca: Colonia Saint Jordi, 50 km SE Palma, 15.IX.2007, M. Ramírez, on walls of houses, collected as immatures, reared to maturity in lab, 2 males 1♀ (MACN-AR; temporary mounts CJG-654–656). Teruel: Molinos, IV. 1985, J. Moles leg., 1 male (MACN-Ar; temporary mounts CJG-561, ARAMR000948).

*Fissarena castanea** (Simon) (Trochanteriidae). AUSTRALIA: Western Australia: 80 km S Port Hedland, 21°00′36″S 118°41′00″E, pitfall trap, side HDF3, 30.IV–9.V.2001, R. Teale, 1♀ (WAM 99/646; SEM preparations MJR-586–588). 43 km S Port Hedland, 20°42′00″S 118°38′24″E, pitfall trap, side HDG2, 30.IV–9.V.2001, R. Teale, 2♂ (WAM 99/644-5; SEM preparations MJR-589–590). OTHER SOURCES: Platnick (2002), retreat and prey-catching behavior of *F. ethabuka* from Henschel et al. (1995).

*Galianoella leucostigma** (Mello-Leitão) (Gallieniellidae). ARGENTINA: Salta: 6 km NW Calafate, 10.I.1995, P. Goloboff and C. Szumik, 1♀ (IML, identified by P. Goloboff, SEM preparations MJR-876, 877, 912); Chuscha, 6 km NO Calafate, 20.XI.1991, P. Goloboff 1♂ (IML, identified by P. Goloboff, SEM preparation MJR-878); Chuscha, 6 km NW Cafayate, 17.VII.1995, M. Ramírez and P. Goloboff, 2 immatures, two eggsacs (MACN, respiratory system examined).

*Gayenna americana** Nicolet (Anyphaenidae). CHILE: Talca: Alto de Vilches, elev. 1180 m, 35°36′S 71°04′W, 14.15.XI.1993, N. Platnick, K. Catley, M. Ramírez, T. Allen, 3♂ 2♀ 5 immatures (AMNH; SEM preparations MJR-282–285); Concepción: Periquillo, 6.XI.1994, T. Cekalovic, 1♂ (AMNH; SEM preparation MJR-605); Parque Nacional Alerce Andino, 100 m, 41°35′S, 72°41′S, 23.XI.1993, N. Platnick, K. Catley, M. Ramírez, T. Allen, 1♂ (AMNH; SEM preparation MJR-281).

*Geraesta hirta** Simon (Thomisidae). MADAGASCAR: Antsiranana: Montagne d'Ambre, 12°30′57″S 49°11′04″E, 12.VIII.1992, V. and B. Roth, 1male 1♀ (CAS; SEM preparations MJR-501–507); 1♂ 2 immatures (CAS, respiratory system examined from immature); 12°30′57″S 49°11′04″E, 12.VIII.1992, V. and B. Roth, 1♂ 1♀ (CAS); 2.79 air km NE of Park entrance, forest, 12°32′S 49°10′E, ca. 1000 m J. Coddington, C. Griswold, N, Scharff, S. Lacher, R. Andriamasimanana, 1♀ (CAS).

Gnaphosa sericata (L. Koch) (Gnaphosidae). MEXICO: Nayarit: San Blas, 12.VI.1956, B. Malkin, ♀ (AMNH; SEM preparations MJR-323–328); San Luis Potosí: 10 mi N of Valles, 23.VII.1945, A.M. Dame, ♂ (AMNH; SEM preparation 330); USA: Texas: Pearsall, 9.VII.1936, L. Davis, ♀ (AMNH; SEM preparation MJR-329, spinnerets with piriform silk coming out).

*Gnaphosa taurica** Thorell (Gnaphosidae). KIRGHIZSTAN: Kirghiz-Ata gorge, Northern slop, June 11, 1985, Coll. A.A. Zyuzin, ♂♀ (Ovtsharenko private collection; SEM preparations MJR-750–754, temporary mounts CJG-357–359).

*Griswoldia acaenata** (Griswold) (Zoropsidae). SOUTH AFRICA: Western Cape: Kranshoek, 20 km E Knysna, forest, 30°05′S 23°14′E, elev. 180 m, 13.XII.1996, C. Griswold, 4♂ 13♀ 5 juv. (CAS, identified by C. Griswold, voucher D. Silva Dávila study 2000; SEM preparation MJR-495, respiratory system examined from immature). OTHER SOURCES: Griswold (1991).

*Heteropoda venatoria** (Linnaeus) (Sparassidae). DOMINICAN REPUBLIC: no specific locality, IV.20. M2, a3907, 1♀ (AMNH; SEM preparations MJR-114–119); Sánchez, 22–27.V.1915, (AMNH; SEM preparations MJR-120, 121, eyes dissected). OTHER SOURCES: Jäger and Ono (2000), Jäger (2001).

Hispo sp.* (Salticidae). MADAGASCAR: Mahajanga, P. Nat. Tsingy de Bemaraha, 3.4 km 93°E Bekopaka, Tombeau Bazimba, 6–10.XI.2001, 19°8′31″S, 44°49′41″E, elev. 50 m, tropical dry forest, general collecting night spiders, B.L. Fisher et al., BLF4339, 1♂ 14♀ 6 immatures (CASENT 9009000; SEM preparations MJR-783–786, preparations JXZ95–101, 111–116, ARAMR000910). OTHER SOURCES: Wanless (1981).

Holcolaetis cf. *zuluensis** (Salticidae). ZIMBAWE: Malene Dam, Matopos 2028D1 E. Pinkey found preying on *Selenops* (num 2/A454), 14.III.1980, (NMZ/A 10692; SEM preparations MJR-427–432, eyes dissected); Murambinda, Buhera, 10.X.1986, P. Hindley, 1♂ (NMZ/A 5302); 1932DL, Sayamiti School, 24.X.1987, T. Bando, (NMZ/A 6424; SEM preparations MJR-433, 434). Identified by Wijesinghe, 1994.

Homalonychus selenopoides Marx (Homalonychidae). USA: Arizona: Tucson Mts., 1.I.1936, O. Bryant, 1♀ (AMNH; respiratory system examined).

Homalonychus theologus Chamberlin (Homalonychidae). USA: California: Carrizo, Wash nr. Picacho, Imperial Co., 25.I.1959, W. Gertsch, V. Roth, 1♀ (AMNH, identified by Roth and Brown, 1974; SEM preparations MJR-338–342); 2 mi W Picacho, Imperial Co., 30.XII.1959, V. Roth, 1♂ 1 immature (AMNH, identified by Roth and Brown, 1974; SEM preparation MJR-343). San Bernardino Co., 1 mi N Earp off Parker Dam Road, N34.10.924 W 114.18.023, elev. 500 ft, 3.XI.2001, M. Hedin, P. Paquin, S. Crews, J. Starret, M. Amaladas, MCH 01_222, collected at night in large wash, 1♂ (AMNH, ex SDSU, voucher for DNA extraction in AMNH SP0075 Hoth; SEM preparation MJR-421); Maricopa Co., Maricopa Mts., cf. N Maricopa Mts. Wilderness, Butterfield Trail, N 33.01.575 W 112.29.364, elev. 600 ft, 23–24.XI.2001, M. Hedin, MCH 01_227, under rocks-flats, washes, hillsides, 1♀ (AMNH, ex SDSU; SEM preparations MJR-422, 423). Arizona: Maricopa Co., Maricopa Mts., cf. N Maricopa Mts. Wilderness, Butterfield Trail, N 33.01.575 W 112.29.364, elev. 600 ft, 23–24.XI.2001, M. Hedin, MCH 01_227, under rocks-flats, washes, hillsides, (MACN, ex SDSU; temporary setting for live animal MJR-562).

*Hortipes merwei** Bosselaers and Jocqué ("Liocranidae"). SOUTH AFRICA: KwaZulu-Natal: St Lucia Game Reserve, Fanies Island, elev. 23–30 m, S28°06′36.8″ E 32°25′52.5″, 31.III–4.IV.2001, M. Ramírez, 7♂ 2♀ (MACN-Ar; SEM preparations MJR-858–862). OTHER SOURCES: Bosselaers and Jocqué (2000).

Hovops sp.* (Selenopidae). MADAGASCAR: Mahajanga, P. Nat. Tsingy de Bemaraha, 3.4 km 93°E Bekopaka, Tombeau Bazimba, 6–10.XI.2001, 19°8′31″S, 44°49′41″E, elev. 50 m, tropical dry forest, general collecting night spiders, B.L. Fisher et al., BLF4339, 1♀ 4 immatures (CASENT 9008829; SEM preparations MJR-778–780, temporary mount MJR-869). Fianarantsoa: Forêt d'Andalalava, 29.6 Km 280°W Ranohira, 22°35′30″S, 45°07′42″E, 700 m, dry forest on sandy soil, general collecting, beating, puffing spiders, 1–5.II.2003, col. Fisher, Griswold et al., BLF7390, 2♂ 2♀ 2 juv. (CASENT9015952).

Huttonia palpimanoides O. P.-Cambridge (Huttoniidae). NEW ZEALAND: Otago, Trotters Gorge, from ferns, 6.II.1979, R.R. Forster, 1 immature (NMNH; respiratory system examined). OTHER SOURCES: Forster et al. (1984).

Huttonia sp. (Huttoniidae). NEW ZEALAND: Kapiti Island, off SW Coast of North Island, 40°52′S 174°55′E, ex pitfall trap D.10, 1996, J. Mclartney, 1♀ (CAS, spermathecae examined).

Huttonia sp.* (Huttoniidae). NEW ZEALAND: North Island: Wellington, Orongorongo Res. Project, 5B Pit 3 OUFS, 1.VI.1992, ♀ (OMD; SEM preparations MJR-827–829); 1♂ (OMD; SEM preparation MJR-830).

*Hypochilus pococki** Platnick (Hypochilidae). USA: North Carolina: Swain Co., Great Smokey Mountain National Park, Deep Creek Campground, ca. 0.3 km along Stone Pile Trail, 35°27.848′N 83°26.078′W, J. Bond & F. Coyle, 19.X.2002, 585 m, 1 male 1♀ (AMNH, identified by J. Bond, 2002; SEM preparations MAI-115–122, MJR-00863, temporary preparations PMF-28–32, CJG-53, 64, ARAMR000641, 642); Haywood Co., Above Crabtree to Betsey's Gap, 3956′, 3.X.1960, W. Gertsch, W. Ivie, many specimens, (AMNH; SEM preparations MJR-735, 836, 837); Jackson Co., Wolf Cr., 5 mi S Chilowhee, on Cull Mtn. Rd., elev. 2200 m, rock outcrop, 2.V.1999, F. Coyle, early spiderlings (MACN-Ar, identified by Fred Coyle; SEM preparations MJR-29–31, 59).

Jacaena sp.* (Liocranidae: *Teutamus* group). VIETNAM: Ha Tinh: Huong Son District, An River, Huong Son Forest, 13 Km W Rt. 8, ca. 18°20′52″N, 105°14′41″E, (ref. pi), 680 m, mammalogist's pitfalls, v.15.1998, D. Silva Dávila, 1♂ 1♀ (AMNH; SEM preparations MJR-415–420); same data, (ref. HS24) 680 m, mammalogist's pitfalls, v.17.1998, D. Silva Dávila, 5♂ 2♀ (AMNH); same data, (ref. HS9) 230 m, around camp, v.22.1998, D. Silva Dávila, 2♂ 1♀ (AMNH).

*Lampona cylindrata** (L. Koch) (Lamponidae). AUSTRALIA: Western Australia: Eucla, 31°43′S 128°54′E, donated II.1986, unknown collector, 3♂ 2♀ (WAM 96/1427-30; SEM preparations MJR-380–386, posterior respiratory system examined from male). OTHER SOURCES: Platnick (2000), prey behavior from Forster (1979).

*Lamponella brookfield** Platnick (Lamponidae). AUSTRALIA: Queensland: South East Queensland, Stony Ck., via Sanford, 27°20′S 152°48′E, 2.II–8.IV.1995, H. Janetzki & G. Monteith, pitfall trap, rainforest, det. Norman Platnick, 1♂ (QMS50084); Perry's Knob, 200 m, 13.I–16.V.1999, G.B. Monteith, pitfall, vine scrub, 1♀ (QMS52462; SEM preparations MJR-1311–1313); Buhot Ck., Burbank, 27°35.5′S 153°10.3′E, 500 m, 2–31.X.2003, QM party, pitfall trap, riparian forest, 51641, 1♂ (QMS67146; SEM preparation MJR-1314); Buhot Ck., Burbank, 27°35.5′S 153°10.3′E, 50 m, 1.XII.2003–1.I.2004, QM party, pitfall trap, riparian forest, 51798, 1♀ (QMS67147, tapetum observed); South East Queensland, Baehr's Scrub, 27°45′S 153°10′E, 100 m, 10.XII.1991–21.I.1992, D.J. Cook, Rf pitfall, det. Norman Platnick 1999, 1♀ (QM25031).

*Lauricius hooki** Gertsch (Tengellidae). USA: New Mexico: San Miguel Co., Windy Bridge picnic area, 8 mi N Pecos, Rt 63, on rock outcrops at night, 17.VIII.1992, K.M. Catley and D. Loch, 1♂ 1♀ (AMNH; SEM preparations MJR-94–101); Lincoln Co, nr. Sierra Blanca Park, Oak Grove Campground, 9480 ft, 32°24′N 105°45′W, V. and B. Roth, 5♂ 1♀ 1 immature (AMNH); Mimbres Mountains, Rock Creek Camp, 32°54′N 107°45′W, 7.IX.1941, W. Ivie, 1♂ 1♀ (AMNH). Identified by K.M. Catley.

Lauricius sp. (Tengellidae). ARIZONA: Rustler Park, Chiricahua Mts., 109°16′W 31°51′N, 23.V.1963, W, J, Gertsch and W. Ivie, 1♀ with eggsac (AMNH; eggs, SEM preparation MJR-93).

*Legendrena perinet** Platnick (Gallieniellidae). MADAGASCAR: Fianarantsoa: P. Nat. Ranomafana: fan-trap, IV.1992, V. and B. Roth, 3♂ 3♀ (CAS; SEM preparations MJR-331–336); 2.3 km N Vohiparara village, 21°12.8′S 47°23.0E, ca 1100 m, pitfall traps, 10–28.IV.1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, E. Rajeriarison, J. Ranoriaranarisoa, J. Schweikert, D. Ubick, 10♂ 2♀ (CAS). Respiratory system from probable immature partially digested in the trap liquid.

*Lessertina mutica** Lawrence (Eutichuridae). SOUTH AFRICA: Eastern Cape, Kei Mouth, 32°41.280′S 28°22.484′E, 12.XII.2002, litter, coastal dune forest, C. Haddad 1♂ 1♀ (MACN-Ar 10795; preparations CJG-499, 500, MJR-1093–1098, 1326–1327; ARAMR000555, ARAMR000931).

*Liocranoides unicolor** Keyserling (Tengellidae). USA: Tennessee: Sumner Co., Fox Cave, Castalian Springs, 24.III.1949, Jones and Archer, 3♀ several immatures (AMNH; SEM preparations MJR-521–523, respiratory system examined from ♀ and immature); Smith Co., Piper Cave, 5.II.1961, T.C. Barr, 1m 1♀ (AMNH; SEM preparations MJR-524, 525). Identified by N. Platnick, 1999. Other sources: Platnick (1999), Silva Davila (2003).

*Liocranum rupicola** (Walckenaer) (Liocranidae). BELGIUM: Remouchamps, 26.IV.1932, J.R.F. Colette, 1♀ (IRSN; SEM preparations MJR-484–487); Grotte d'Eprave, 26.III.1899, G. Severin, 1♂ (IRSN, "prep. No. 15"), all identified by J. Kekenbosch, 1958. ITALY: Sempeyre (CN): Becetto, 2.XI.2002, G. Gardini leg., 1♀ (A. Trotta personal collection; SEM preparation MJR-1017). Finale Ligure (SV): Magnone, 3.XI.2002, A. Pesce and A. Trotta, 1♂ (A. Trotta personal collection; SEM preparations MJR-1024, 1025).

Lygromma sp.* (Prodidomidae). VENEZUELA: Lara: P. Nac. Yacambú, 10.5 km SE Sanare, 1760 m, cloud forest litter, 09°41′52″N 69°37′03″W, 1.VI.1998-056C, R. Anderson, 1♂ 2♀ (AMNH; SEM preparations MJR-718–722); 6.4 km SE Sanare, 1850 m, 09°41′51″N 69°38′57″W, 17.V.1998-014, R. Anderson, 1♂ (AMNH; SEM preparations MJR-723–724). Other sources: Respiratory system from *Lygromma simoni* (Berland) (see Ramírez, 1995a), morphology from Platnick and Shadab (1976).

*Lyssomanes viridis** (Walckenaer) (Salticidae). USA: Florida: Martin Co., Along S-76 ca 17 mi E Port Moyaca, beating saw palmetto nr. St. Lucie Canal, 19.IV.1977, B. Richman, 5♂ 1♀, (FSCA, identified by D. Richman; SEM preparations MJR-682–688, respiratory system examined from male). Other sources: Galiano (1962, 1980).

*Macerio flavus** (Nicolet) (Eutichuridae). CHILE: Elqui: 20 km N La Serena (Rt 5 km 491), 120 m, 7.X.1992, N. Platnick, P. Goloboff, K. Catley, 2♀ (AMNH, SEM preparations MJR-5–8, 80). Concepción: Escuadrón, elev. 5 m, 36°57′S 73°09′W, 18.XI.1993, N. Platnick, K. Catley, M. Ramírez, T. Allen, 2 males (AMNH, SEM preparation MJR-81). Malleco: Monumento Natural Contulmo, 12.I.1989, M. Ramírez, 5♀ (MACN; respiratory system examined, photo MJR-37(4)). Other sources: Ramírez et al. (1997).

*Macrobunus multidentatus** (Amaurobiidae: Macrobuninae). CHILE: Chiloé: Arroyo Cole Cole, 25 km N Cucao, 8–11.II.1991, M. Ramírez, 2 males 1♀ (MACN-Ar; SEM preparations MJR-958–962); 15 km S Chepu, 3.II.1991, M. Ramírez, 2 immatures (MACN; respiratory system and tapeta examined).

*Malenella nana** Ramírez (Anyphaenidae). CHILE: Concepción: Cerro Caracol, Concepción, elev. 200 m, 36°51′S, 73°02′W. 17.XI.1993, N. Platnick, K. Catley, M. Ramírez, T. Allen, 2♀ (AMNH). Cautín: Cerro Ñielol, Temuco, I.1989, M. Ramírez, 1♀ (MACN; respiratory system examined, same specimen as in Ramírez, 1995: fig. 1). Other sources: Ramírez (1995).

*Mandaneta sudana** (Karsch) ("Corinnidae" incertae sedis). GHANA: Ada Foah, Volta River Basin, Ungar col., ZMB 2143, male holotype. CÔTE D'IVOIRE: Bettié, forêt classeé de Mabi, dense forest, by hand, 26.XI.1993. R. Jocqué, 1♀ (MRAC 177.640; SEM preparations MJR-574–576); same locality, Eco. grappe 3, 24.III.1997, T. Steyn, 1♀ (MRAC 207387); Appouesso, FC Bossematié, Forest, pitfall, station 1B, 12.II.1995, R. Jocqué and R. Tanoh, 1♀ (MRAC 204.306); same locality, station 5, found in leaf litter, 21.III.1997, T. Steyn, 1♂ (MRAC 207386).

*Medmassa semiaurantiaca** Simon (Corinninae: Castianeirinae). KENYA: Rift Valley: West Pokot District, Marich Pass Field Studies Centre, 3000 ft., 1°32.2′S, 53°27.4′E, 7.VI.1999, W.J. Pulawski and Schweikert, 2♂ (CAS; SEM preparations MJR-570, 571); ETHIOPIA: Alomata, 500 ft., 16.I.1960, E.S. Ross, 1♀ 1 penultimate ♀ (CAS; SEM preparations MJR-572, 573, respiratory system from penultimate ♀). OTHER SOURCES: Haddad and Bosselaers (2010).

*Meedo houstoni** Main (Gallieniellidae). AUSTRALIA: Western Australia: Boolathana Station, 24°24′48.7″S 113°44′40.6″E, 20.VIII–30.IX.1992, BO4, A. Sampey et al., wet pits, WAM/CALM Camarvon Survey, 1♀ (WAM 94/264; SEM preparations MJR-591–593); 15.I–31.V.1995, wet pits, J.M. Ealdock et al., 2♀ (WAM 99/281-2; respiratory system examined); Bush Bay, site BB 3, wet pits, 25°04′39.8″S 113°42′36.9″E, 10.VIII–30.IX.1994, M.S. Harvey et al., WAM/CALM Carnarvon survey, 2♂ 2♀ (WAM 99/277-4; male eyes dissected). OTHER SOURCES: Platnick (2002).

*Megadictyna thilenii** Dahl (Nicodamidae). NEW ZEALAND: North Island: Moerangi, 625 m, mixed podocarp forest, ber. For. litter, 4–9.VI.1980, A. Newton and M. Thayer, 1♂ (AMNH; voucher D. Silva Dávila study 2000); Tuna Saddle, N of Taumaranui, 10.I.1967, R.R. Forster, 1♀ (AMNH; voucher D. Silva Dávila study 2000). OTHER SOURCES: Forster (1970b), Harvey (1995).

*Meriola barrosi** (Mello-Leitão) (Trachelidae). CHILE: Bío Bío: W Ralco, Santa Bárbara, 400 m, 22–23.XI.1994, L. Peña, 4♂ 8♀ (AMNH; SEM preparations MJR-10–16, 18, 26, 28); Valdivia: Lago Calafquen, Casa de Piedra, 20.II.1994, T. Cekalovic, 6♂ 8♀ (AMNH; SEM preparations MJR-26, 27). OTHER SOURCES: Platnick and Ewing (1995).

*Metaltella simoni** (Keyserling) (Amphinectidae: Metaltellinae). USA: Lousiana: St. Tammany Co., Pearl River, 196x, 3♂ 11♀ (AMNH, identified by R. Leech, X.1970); 1965 (?), L. Roddy, 2♂ 2♀ (AMNH). ARGENTINA: Buenos Aires: Villa Madero, VIII.1998, C. Scioscia, 1 male (MACN-Ar); Entre Ríos: El Palmar, XI.1988, M.E. Galiano 1 male (MACN-Ar). OTHER SOURCES: Davies (1998).

*Micaria fulgens** (Walckenaer) (Gnaphosidae). BELGIUM: As, 12.V.1958, J. Kekenbosch, 1♂ 1♀ (IRSN IG 21277; SEM preparations MJR-656–660, 710); Logne, 30.IV.1957, J. Kekenbosch, 3♂ (IRSN; SEM preparations MJR-661, 689, 690). All identified by J. Kekenbosch.

*Mimetus hesperus** Chamberlin (Mimetidae). USA: Nevada: Lander Co., Kingston Camp, 30 mi S Austin, Toiabe Range, 3700 ft, 12.VIII.1966, F.P. and M. Rindge, 2♀ (AMNH; SEM preparations MJR-823, 824); Arizona: Brown Canyon, Baboquivari Mts., 9.VII.1952, M. Casier, W. Gertsch and Schramak, 1♂ (AMNH). MEXICO: San Luis Potosí: Valles, 19.VII.1956, W. Gertsch, V. Roth, 1♀ (AMNH; SEM preparation MJR-825). All identified by D.J. Mott, 1986–1987. OTHER SOURCES: Griswold et al. (2005).

*Mituliodon tarantulinus** (L. Koch) (Miturgidae). AUSTRALIA: Tasmania: Risdon, 4.VI.1945, V. Hickman, 4♂ (AMNH; SEM preparation MJR-509); New South Wales: 11 km NE Bulahdelah, ca. 50 m, O'Sullivan's Gap Res., 11.VI–27.VIII.1982, FIT, wet sclerophyll, S. and J. Peck, 1♀ (AMNH; SEM preparations MJR-509–511); Queensland: Gayndah, Burnett R., near river in wooded area, 25°37′16.6″S 151°36′17.6″E, 22.XI.1998, D. Silva Dávila, 3♀ (AMNH, vouchers Silva Dávila study 2000; respiratory system examined). OTHER SOURCES: Griswold (1993), Silva Davila (2003), Raven and Stumkat (2003).

Miturga cf. *lineata** (Miturgidae). AUSTRALIA: Western Australia: Bungalbin Hill, 30°18′S 119°43′E, pitfall traps, 1–6.XII.1981, W.F. Humphreys et al., 1♂ 1♀ (AMNH ex WAM, identified by D. Silva Dávila, 1998; SEM preparations MJR-710–714). Queensland: Dargonelly Rock Holes, Mt. Moffat, 29.IX.1986, M. Bennie, 1♂ 2 immatures (QMB S15982; respiratory system examined from immature); SW track L. Broadwater, nr. Dalby, web in log, 22.XI.1987, M. Bennie, 1♀ (QMB S3323).

*Miturga gilva** L. Koch (Miturgidae). AUSTRALIA: Queensland: Townsville, 3–6.II.1945, B. Malkin, 2♂ 4♀ 8 juv. (AMNH; SEM preparations MJR-489–494, 911, respiratory system examined from immature, identified by Robert Raven from images, in litt.). New South Wales: Fowlers Gap, V.1975, no collector, 1 male (QM S39047, det. K. Stumkat); L. Broadwater, SEQ, near light trap, 11.XI.1984, M. Bennie, 1♀ (QMB S39071, det. K. Stumkat).

Miturga lineata Thorell (Miturgidae). AUSTRALIA: Queensland: trade to N end Lake Broadwater, M. Bennie, J. Thompson, 19.II.1985, 1♀ (QMS 32938, SEM images thanks to Diana Silva Dávila, voucher data in litt); SW track, L. Broadwater, nr. Dalby, web in log, 22.XI.1987, M.

Bennie, 1♀ (QMS3323; temporary mounts CJG-543, 544); Dargonelly Rock Hole, Mt. Moffat, 29.IX.1986, M. Bennie, male (QMS15982; temporary mount CJG-545).

Miturgidae QLD* (Miturgidae). AUSTRALIA: South Australia: 14 Km WNW Renmark, 33.535S 140.44E (GPS), Mallee on dune, pitfall trap, 2.V.1995–7.VI.1995, K.R. Pullen, 1♀ (QMB S41780; SEM preparations MJR-480–483, 1007); 32 Km N Renmark, 33.535S 140.44E (GPS), flight/ground intercept trap, 29.III.1995–3.V.1995, K.R. Pullen, 6♂ (QMB S39098; SEM preparations MJR-478, 479).

*Neato walli** Platnick (Gallieniellidae). AUSTRALIA: Victoria: Barr Creek, Cohuna, watering, 35°49′S, 144°11′E, 1.V. 1999, J. Hooper, D., J. Shield, J. Woodman, 2♂ 1♀ (CVIC 738, identified by N. Platnick; SEM MJR-994). OTHER SOURCES: Platnick (2002).

*Neoanagraphis chamberlini** Gertsch and Mulaik ("Liocranidae"). USA: Nevada: *Nye Co.,* Nevada Nuclear Test Site, 1BF15C, 15.60, 1♂ (AMNH, identified by R. Vetter, 2000); 11. VIII.1961, (BYU-AEC-NTS, H or S, Code 1FL10(c)) 1♂ (AMNH; SEM preparations MJR-50, 843); 15.VI.1965, (BYU-AEC-NTS, H or S, Code 10W(c)) 1♀ (AMNH; SEM preparations MJR-1–4); 15.VI.1965, (BYU-AEC-NTS, H or S, Code 10W(c)) 1♀ (AMNH; SEM preparations MJR-44–46). Texas: Presidio Co., ex burrows of *Cratogeomys castonops* VIII.1998, G.C. Menzies, 1♀ (AMNH; SEM preparation MJR-842). All identified by R. Vetter, 1997–2000.

*Neoramia charybdis** (Hogg) ("Agelenidae," member of the Austral Cribellate Clade, see Miller et al., 2010). NEW ZEALAND: South Island: Goden Bay, 15.XI.1961, R.R. Forster, 2♀ 1 immature (AMNH, identified by R. Forster). Stewart Island, Big South Cape, no date, R.K. Dell and B. Holloway, 1♂ (AMNH, identified by R. Forster). OTHER SOURCES: Forster and Wilton (1973), Griswold et al. (2005).

*Neozimiris pubescens** (Banks) (Prodidomidae). USA: California: Riverside Co., Cactus city, 1800 ft., 10 mi W Chiriaco summit off I-10, in pitfall, 5.IV.2000, R. Vetter, 1♂ (AMNH; SEM preparations MJR-735, 736); Cactus city, 11 mi W Chiriaco summit off I-10, in pitfall, collected 20.III.2001, matured VI.2001, R. Vetter, 1♀ (AMNH; SEM preparations MJR-738–741, 766); same data, 400 m, 20.III.2001, 2♂ (AMNH). OTHER SOURCES: Platnick and Shadab (1976c).

*Nicodamus mainae** Harvey (Nicodamidae). AUSTRALIA: Western Australia: Coalseam Park, Miners picnic site, by head-torch at night, under rock, Irwin River Bank, 29°01′S 115°29′E, 11.XI.1999, J.W. Waldock, 1♀ (AMNH; SEM preparations MJR-678–680, 813); Bush Bay, site BB 4, 25°06′49″S 113°43′52″E, (GPS), 28.IX.1998, M.S. Harvey et al., WAM/CALM survey, 1♂ (AMNH; SEM preparation MJR-681, temporary mount MJR-870). Both specimens identified and donated by M. Harvey, 2001. OTHER SOURCES: Forster (1970b), Harvey (1995).

Nops sp. (Caponiidae). BRITISH VIRGIN ISLANDS: Little Jost Van Dyke, 27.VII.1965, Island Project Staff, Univ. of Puerto Rico ♀ (AMNH; SEM preparation MJR-147).

*Odo bruchi** (Mello-Leitão) (Miturgidae: *Xenoctenus* group). ARGENTINA: Santiago del Estero, P. Nac. Copo, 26°04′S, 61°44′W, pitfall, 23–25.X.2003, F. Cuezzo 1♀ (MACN-Ar; tapetum visible). La Pampa: P. Nac. Lihué Calel, ca. 300–400 m, 25–28.VIII.2003, M. Ramírez, A. Ojanguren, F. Labarque, A. Ravelo, 1♂ 1♀ (MACN-Ar 10390; SEM preparations MJR-1079–1088); Buenos Aires: Abra de la Ventana, X.1969, Cordelotti col., 1♀ (MACN-Ar; temporary preparations PMF-78–80); Sierra de la Ventana, Cerro Negro, 12.XI.1974, Cesari col., 1♂ 1♀ (MACN-Ar; male temporary preparations PMF-76, 77). This species is very similar to *Odo galapagoensis* (see Baert, 2009).

*Oecobius navus** Blackwall (Oecobiidae). USA: Georgia: 1 mi N Sylvania, 10.IV.1943, W. Ivie, 4♂ 4♀ (AMNH, identified by W. Ivie as *O. parietalis*; SEM preparation MJR-826). New York: New York, 28.X.2002, M. Ramírez (MACN). OTHER SOURCES: Baum (1972), Griswold et al. (2005).

Oedignatha cf. *jocquei** (Liocranidae: *Teutamus* group). VIETNAM: Ha Tinh: Huong Son District, An River, Huong Son Forest, 13 Km W Rt. 8, ca. 18°20′52″N, 105°14′41″E, (ref. beta) 230 m, v.6.1998, D. Silva Dávila, 1♀ (AMNH/IEBR; SEM preparations MJR-222, 223, 841); same data, (AMNH/IEBR; SEM preparations MJR-105, 106); same data, (ref. HS31) 680 m, mammalogist's pitfalls, v.12.1998, 1♂ (AMNH/IEBR; SEM preparations MJR-224, 840); same data (ref. HS1), 940 m, v.15.1998, 1♂ (AMNH/IEBR).

Oedignatha sp. (Liocranidae: *Teutamus* group). SEYCHELLES: Mahe Centre, Bon Espoir, Eco. 300 m, touffes de graminnées sur glacis, 21.VI.1972, P.L.G. Benoit and J.J. Van Mol, 5♂ 9♀ 15 immatures (MRAC 143.228; ♀ respiratory system examined).

*Olbus jaguar** Ramírez et al. ("Corinnidae" incertae sedis). CHILE: Malleco: Monumento Natural Contulmo, 13.II.1992, M. Ramírez, N. Platnick, P. Goloboff, 1♂ 1♀ (AMNH); Osorno: 36 km W La Unión, 600 m, 25–28.III.1987, L. Peña, 2♀ (AMNH); Osorno: Maicolpué, 64 km W Osorno, 19.II.1992, N. Platnick, M. Ramírez, P. Goloboff, 1♂ (MACN-Ar). Palena: 37 km SE Chaitén, 28.XII.1984–30.I.1985, S. y J. Peck, 1♂

(AMNH). Chiloé: Chepu, 21.II.1992, N. Platnick, M. Ramírez, P. Goloboff, 1♂ 1♀ (MACN-Ar 16709; ♀ leg III, IV and ♂ abdomen imaged with SEM for Ramírez et al., 2001). OTHER SOURCES: Ramírez et al. (2001).

*Orthobula calceata** Simon (Phrurolithidae). ZIMBAWE: Batoca Gorge & Dibu Dibu River, 17°58′S, 25°57′E, 27–28.X.1990, V.D. & B. Roth 6♂ 2♀ 1♀ subadult (CAS; SEM preparations MJR-235–241).

Otacilia sp.* (Phrurolithidae). VIETNAM: Ha Tinh: Huong Son District, An River, Huong Son Forest, 13 Km W Rt. 8, ca. 18°20′52″N, 105°14′41″E, (ref. HS3) 680 m, entomologists pitfalls, v.17.1998, D. Silva Dávila, 1♀ (AMNH/IEBR, SEM preparations MJR-408–412); (ref. HS1), 940 m, mammalogists pitfalls, v.15.1998, D. Silva Dávila, 2 males (AMNH/IEBR, SEM preparations MJR-413–414); (ref. HS62) ca. 300 m, main trail, night, iv.12.1998, D. Silva Dávila, 4 males 1♀ (AMNH/IEBR); (ref. HS81) ca. 300 m, main trail, night, iv.17.1998, D. Silva Dávila, 1♀ 1 immature (AMNH/IEBR, respiratory system examined from immature).

*Oxyopes heterophtalmus** (Latreille) (Oxyopidae). TURKEY: Anatoile Meridional, Marmaris (Kill. Mugla), V.1969, G. Fagel, 1♀ (IRSN; SEM preparations MJR-621, 845–847). GREECE: Crete, Hiraklion, nr. Kassabo, Kassabonos Valley, 25.IV.1931, A. D'Orchymont, 1♂ (IRSN; SEM preparation MJR-622). ITALY: Troina, Fiume di Sotto, 6.V.1968, S. Langemark, 2♂ (ZMUK).

Paccius cf. *scharffi** (Trachelidae). MADAGASCAR: Fianarantsoa: P. Nat. Ranomafana: Talatakely 21°14.9′S, 47°25.6′E, 5–18.IV.1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, J. Ranoriaranarisoa, J. Schweikert, D. Ubick, 4♂ 3♀ 3 immatures (CAS; SEM preparations MJR-348–356, ARAMR000176, 176, 178), 3♂ 2♀ (CAS).

*Paradiestus penicillatus** (Mello-Leitão) (Corinnidae: Corinninae). ARGENTINA: Misiones: Refugio Piñalito, XI.1954, R. Schiapelli, M.E. Galiano, 2♂ 1♀ (MACN-Ar; SEM preparations MJR-1210–1212; temporary mount MAI-110; ARAMR000997); P. Prov. Salto Encantado, sendero al Salto Escondido, S27°07′ W54°48′, 11–12.I.2005, collected while eating a conspecific male, identified by Bonaldo from photograph, C. Grismado, L. Lopardo, L. Piacentini, A. Quaglino & G. Rubio col., 1♀ (MACN-Ar, temporary mount CJG-263); P. Nac. Iguazú, Sendero Macuco, área Cataratas, I.1993, M. Di Vitteti 1♀ (MACN-Ar; SEM preparations MJR-1213–1218, MAI-101, 112; ARAMR000996); Deto. San Pedro, P. Prov. Cruce Caballero, S 26°28′O 53°58′, 13–16.I.2005, C. Grismado, L. Lopardo, L. Piacentini, A. Quaglio & G. Rubio, 1♂ (MACN-Ar; SEM prepartions MAI-74, 75; ARAMR000183). OTHER SOURCES: Bonaldo (2000).

Paravulsor sp.* (Miturgidae: *Xenoctenus* group). ARGENTINA: Misiones: PN Iguazú: Sendero Macuco, S25°40′45.2″ W54°26′57.4″, 250 m, 16–20 May 2005, M. Ramírez, P. Michalik, F. Labarque 1♀ (MACN-Ar; temporary preparation CJG-498; ARAMR000930; photos taken); same data, 1♂ (MACN-Ar; temporary preparation CJG-497; ARAMR000929; matured in lab, preserved 15.VII.2005); same data, 1♂ (MACN-Ar 10807; SEM preparations MJR-1135 – 1137); same data, 1♀ (MACN-Ar 10806; SEM preparations MJR-1128 – 1134); Parque Nacional Iguazú: área Garganta del Diablo, S25°42′16,7″, W54°26′28,2″, 250 m, 16–20 May 2005, M. Ramírez, P. Michalik, F. Labarque, 1♀ (MACN-Ar; temporary preparation PMF-18–20; ARAMR000606); Parque Nacional Iguazú: Ruta 101 5 Km E arroyo Yacui, S25°41′02,3″, W54°11′57.1″, 310 m, 18 May 2005, M. Ramírez, P. Michalik, F. Labarque, 1♂ (MACN-Ar; temporary preparation PMF-16–17; ARAMR000605). Identified by comparison with images from Rio de Janeiro spider inventory, determined by Renner Baptista.

Pardosa moesta Banks (Lycosidae). USA: New Hampshire: Epping, on grass, 12.V.2001, M. Townley, 1♂ (University of New Hampshire; SEM preparations MJR-853, 854).

Petrichus sp.* (Philodromidae). ARGENTINA: Río Negro: Cerro Ne-Luan, I.1975, E. Maury, 9♀ 5 immatures (MACN, SEM preparations MJR-926–929, respiratory system and eyes examined from immature); Mendoza: Coipolauquen, I.1975, E. Maury, 1 male (MACN). NOTE: It is not clear that male and females belong to the same species.

*Philodromus aureolus** (Clerck) (Philodromidae). USA: Idaho: Payette (north side of town), W116°56′ N44°5′, 20.I.1953, W. Ivie (AMNH, identified by W. Ivie, 1954; SEM preparation MJR-155). POLAND: Milanówek, woj. Warszawskie, 8.VI.1990. B. Malkin, (AMNH; SEM preparations MJR-181, 182); Lesna woj. Warszawskie, 26.VI.1982, B. and H. Malkin, 1♀ (AMNH; SEM preparations MJR-183–187). DENMARK: NEZ, UB49 Rude Skov, Birkerød, 3.VI.1993, S. Langemark, 1♂ 2♀ (ZMUK 4934; SEM preparations MJR-757, 758).

Philodromus californicus Keyserling (Philodromidae). USA: Oregon: Cline Falls 4 Mi W Redmond Em. 10–20.VI.1952, V. Roth (AMNH; SEM preparation MJR-169)

*Phrurolithus festivus** (C.L. Koch) (Phrurolithidae). BELGIUM: Chokier (Carr. Sacré), MOMR FS 70 st. II, 3.V.1991–21.IV.1992, R. Detry, 6♂ 6♀ (IRSN IG 27748, identified by J. Kekenbosch; SEM preparations MJR-650–655; respiratory system examined). OTHER SOURCES: Whiele (1967a).

*Phrurotimpus alarius** (Hentz) (Phrurolithidae). USA: West Virginia: Monongalia Co. 3–10.VII.1990, WV University Forest, Mixed oak-hardwood, pitfall trap, stand 2 plot 9, D.T. Jennings, 1♀ (AMNH, SEM preparations MJR-227–232); same data, 19–26.VII.1990, stand 4 plot 11, 5 males (AMNH, SEM preparations MJR-233–234).

Phrurotimpus borealis (Emerton) (Phrurolithidae). USA: Illinois: Lake County, Right Woods, Mesic upland forest, 400 m, 30.VI.1998, M. Ramírez, 1 male, 4♀, 2 immatures (MACN).

*Pimus napa** Leech (Amaurobiidae). USA: California: Napa Co., 3 mi W Oakville, 15.II.1954, Roth and Schuster, 4♀ paratypes (AMNH; SEM preparations MJR-761–763); 2 mi W Oakville, 31.XII.1953, 3♂ paratypes (AMNH; SEM preparation MJR-764); Mendocino Co., 4.2 mi S Piercy, 17.II.1967, V. Roth, ♂♂ ♀♀ paratypes (AMNH). OTHER SOURCES: Leech (1972), Griswold et al. (2005).

*Platyoides walteri** (Karsch) (Trochanteriidae). SOUTH AFRICA: Mpumalanga: Embuleni Reserve, near Badplaas, 28.III.2001, M. Ramírez, 1♂ 1♀ (MACN-Ar; preparations MJR-1241–1252); same data, 2♀ (AMNH; temporary mount CJG-401; ARAMR000868); same data, 1♂ (MACN-Ar; temporary mounts CJG-399, PMF-200; ARAMR 000792).

*Plexippus paykulli** (Audouin) (Salticidae). USA: Florida: Flamingo, Everglades, reared in lab, ♀ Pp 135B, I.1971, R. Jackson, 2♀ 2♂ (CAS; SEM preparations MJR-772–777, respiratory system examined from male).

*Polybetes pythagoricus** (Holmberg) (Sparassidae). ARGENTINA: Buenos Aires: Zelaya, no date, H. Hepper, 1 male (MACN); José C. Paz, 24.IX.1967, Goldstony, 1♀ (MACN, died 11.VI.1969); Quilmes, Estancia El Dorado, IX.1969, C. Rebollo, 1♀ (MACN). San Pedro, 1.VIII.2006, N. López, 1♂ (MACN-Ar; temporary mounts PMF-1, 2; ARAMR000600). Entre Ríos: Basavilbaso, 11.1947, leg. Accame (A. Bachmann), 1♀ (MACN-Ar 3090; temporary mount CJG-754). Misiones: Dept. San Pedro, P. Prov. Cruce Caballero, S26°28′ W53°58′, 13–16.I.2005, night collecting, in buildings, C. Grismado, L. Lopardo, L. Piacentini, A. Quaglino and G. Rubio, 1♀ (MACN-Ar; SEM preparations FML-311–317; ARAMR000185); same data, 1♂ (MACN-Ar; temporary mount CJG-468; ARAMR000866). Jujuy: San Salvador de Jujuy, XIII.2005, J. Baldo, 2♀ (MACN-Ar; SEM preparation FML-318; ARAMR000865). OTHER SOURCES: Trichobothria from Scioscia (1982).

*Portia schultzi** Karsch (Salticidae). ZIMBAWE: Bulawayo 2028B1, XI.1989, L.H.B. Morris, 1♂ 1♀ (NMZ/A7710; SEM preparations MJR-435–441); Baobab Hill, Hwange, A. Ellert, I.1990, 1♂ 2♀ (NMZ/A 7800). Both identified by P. Wijesinghe, 1994. OTHER SOURCES: Wanless (1978).

Portia sp. (Salticidae). VIETNAM: Con Cuong: (ref. NS12) ca. 600 m, Pumat buffer zone, beating low tree branches, iv.28.1998, D. Silva Dávila, (AMNH; SEM preparations MJR-225, 226).

Procopius cf. *aethiops** ("Corinnidae" incertae sedis). TANZANIA: Tanga: W Usambara Mtns., Mazumbai, station, around buildings, 4°48.5′S 38°30′E, 1500 m, 10–20.XI.1995, C. Griswold, N. Scharff, D. Ubick, 1♂ 1♀ (CAS; SEM preparations MJR-577–581); same data, 4°49′S 38°30′E, 1400–1800 m, 1♂ 1♀ (CAS); E Usambara Mtns., Sangarawe Forest, 5°6.5′S 38°35.7′E, 990 m, 5–6.XI.1995, C. Griswold, N. Scharff, D. Ubick, 1♀ 1 immature (CAS; respiratory system from immature).

*Prodidomus redikorzevi** Spassky (Prodidomidae). TURKMENISTAN: Krasnovodsk area: near Dgebal, mountains, 16.IV.1987, A.A. Zyuzin, 3♀ (SEM preparations MJR-742–747); near Djanga, mountains, 12.IV.1987, T.V. Pavlenko, 1♂ (SEM preparations MJR-748, 749); near Kara-Kala, mountain slop, 12.IV.1987, A.A. Zyuzin, 1♀; near Oglanly, under rocks, 17.IV.1987, A.A. Zyuzin, 1♂. All identified by V. Ovtsharenko, deposited in his private collection.

Prodidomus sp. (Prodidomidae). INDIA: A.P. Tirupati, Nr. Tirumala, 1o1663 JALC, 1 immature (in AMNH; respiratory system examined).

*Pronophaea proxima** (Lessert) ("Corinnidae" incertae sedis). SOUTH AFRICA: Eastern Cape, Kei Mouth, 32°41,280′S 28°22,484′E, 26.XII.2003, litter, coastal forest, C. Haddad, 3♂ 1♂ penultimate (MACN-Ar 10798; SEM preparations MJR-1089–1192, tracheae and tapeta examined from penultimate ♂; det. C. Haddad 2004); 25.9.2004, litter, coastal forest, C. Haddad, 1♂ 1♀ (MACN-Ar; preparations MJR-1043–51).

*Psechrus argentatus** (Doleschall) (Psechridae). PAPUA NEW GUINEA: Camp 1, Menapi, Cape Vogel Peninsula, 21.III–4.V.1953, G. Tate Archbold Exped., 2♂ 2♀ (AMNH, identified by W. Levi, 1979; SEM preparations MJR-462–467). OTHER SOURCES: Levi (1982), Griswold et al. (2005).

*Pseudocorinna felix** Jocqué and Bosselaers ("Corinnidae" incertae sedis). CÔTE D'IVOIRE: Appouesso, FC Bossematié, forest, pitfall, station 5F, 8.X.1995, R. Jocqué and R. Tanoh, 1♂ 1♀ (MRAC 204.320; SEM preparations MJR-563–569); same data, rain forest, pitfall traps, station C, 3.I.1994, R. Jocqué and N. Seabé, 1♀ (MRAC 202.401; respiratory system examined).

Pseudocorinna rutila Simon ("Corinnidae" incertae sedis). Male and female syntypes, from Guinea Bissau, in MHNP, examined.

*Pseudoctenus thaleri** Jocqué (Zoropsidae). MALAWI: Mount Mulanje, Thuchila, 1 Km E van de hut op de krusising Medzeka path en klein beekjie, 11.XI.1981, R. Jocqué, 1♀ (MRAC 156.475; SEM preparations MJR1041, 1042, temporary mount PMF-107). Mount Mulanje, Lichenya plateau Eco., 5–24.XI. 1981, R. Jocqué, 2000 m, on young Cupressus, pitfalls, 2 males (MRAC 156.316; temporary mounts PMF-106, 107).

*Pseudolampona emmett** Platnick (Lamponidae). AUSTRALIA: Queensland: Belmont Hills Bushlands, site 1, 27°30.8′S 153°0.7.1′E, QM Party, 2–29.1.2004, 80 m, pitfall, eucalypt forest, det. M.J. Ramírez, 2007, 2♂ 2♀ (QMS54738; SEM preparations MJR-1305–1309, temporary preparations in clove oil MJR-1315–1317, clarified to observe genitalia and tapetum).

*Raecius jocquei** Griswold (Zorocratidae). No specimens available, scored from Griswold (2000, 2002) and Griswold et al. (2005), and from images by Diana Silva Dávila (personal commun.) from an unidentified species from CAMEROON, Southwest Prov., Fako Div., Mt. Cameroon, nr. Mann's Spring, 2050 m 04°08′30″N, 9°07′01″E, grassland, 21–25.I.1992, Coddington, Griswold, Larcher & Hormiga, 5♀ plus immatures (CAS).

*Rastellus florisbad** Platnick and Griffin (Ammoxenidae). SOUTH AFRICA: Limpopo: Thabazimbi, 14.IX.2005, D. Penney, under logs with termites 1♂ 1♀ (NCA-AcAT 2007/1138). KwaZulu-Natal: Ndumo Game Reserve, 26°53.405′S 18°783′E, 17–27.I.2006, C. Haddad, pitfall traps, 2♂ (MACN-Ar 11390, ARAMR000949, temporary mounts CJG-567–568, preparations MJR-1367–1381; identified by C. Haddad 2006). Other sources: Platnick (1990), Platnick and Griffin (1990).

Scelidocteus vuattouxi Jézéquel (Palpimanidae). BENIN: Banikoara: Chutes de Koudou, "W" Park, N11°40.48′ E03°18.53′, 31.V.2005, 229 m, V. Vignoli & S. Tchibozo ♂♀ (AMNH; SEM preparations MAI-190–197, FML-451, temporary preparations MAI-186, 187, GJG-452, 456, 458).

Segestria florentina (Rossi) (Segestriidae). ARGENTINA: Ciudad Autónoma de Buenos Aires: X.1941, J.M Viana ♂♀ (MACN-Ar SEM preparations MAI-32, 33–43; ARAMR000968, 79, 81); 1967, A. Bachmann, 2♂ 1♀ (MACN-Ar; temporary preparations CJG-662–64, ARAMR000989); 1♂ (MACN-Ar; temporary preparation CJG-611, ARAMR000969).

*Selenops debilis** Banks (Selenopidae). USA: Arizona: Southwestern Res. Sta. 5 miles W Portal, 2–19.V.1956, M. Statham 2♂ 5♀ 1 immature (AMNH; eyes dissected, SEM preparations MJR-193–200, 205); MEXICO: Baja California Norte: 15 S (by Mex. Hwy. 1) of Rosarito, 5.V.1977, R. Seib, 1♂ 2♀ 2 immatures (CAS; SEM preparations MJR-781, 782, respiratory system examined, temporary mounts MJR-867, 868).

Senoculus sp.* (Senoculidae). ARGENTINA: Misiones: San Antonio, dept. Frontera, XI.2954, Schiapelli, De Carlo, Viana, Galiano, 2 males (MACN-Ar 4177, identified by R. Baptista as "*S. purpureus* sensu Schiapelli"; SEM preparations MJR-901–902); P. Nac. Iguazú, XI.1989, M. Ramírez, 1♀ (MACN-Ar 10338, photo MJR-203–205, identified as *Senoculus* cf. *iricolor* by C. Grismado, 2003; SEM preparations MJR-903–904, 953–954). P. Nac. Iguazú, VII.1985, M. Ramírez, 1 subadult ♀ (MACN; respiratory system examined). Other sources: Silva Davila (2003), Griswold (1993).

Sesieutes sp.* (Liocranidae: *Teutamus* group). VIETNAM: Ha Tinh: Huong Son District, An River, Huong Son Forest, 13 Km W Rt. 8, ca. 18°20′52″N, 105°14′41″E, (ref. HS7) 940 m, entomologists pitfalls, v.15.1998, D. Silva Dávila, 8♂ 6♀ (AMNH/IEBR; SEM preparations MJR-400–407).

Sparianthinae VEN* (Sparassidae). VENEZUELA: Mérida: 34 km NW Mérida, Finca "Fundo La Trinidad," 2350 m, 08°37′00″N 71°20′12″W, 027D, montane forest litter, 22.V.1998, R. Anderson, 2♂ 1♀ 8 juv. (AMNH; SEM preparations MJR-537–544, respiratory system from immature).

Stegodyphus sp.* (Eresidae). SOUTH AFRICA: KwaZulu-Natal: Phinda Resource Reserve, elev. 38 m, S 27°50′43″ E 32°18′49.1″, 13–15.IV.2001, M. Ramírez, (MACN-Ar; SEM preparations MJR-767, 768). Other sources: Peters (1992), Griswold et al. (2005).

*Stephanopis ditissima** (Nicolet) (Thomisidae). CHILE: Chiloé: Piroquina, 16.II.1995, T. Cekalovic, 1 male 2♀ (AMNH; SEM preparations MJR-201, 202, 905–907, 932). ARGENTINA: Neuquén: P. Nac. Nahuel Huapi, Lago Espejo, 21.I.1985, M. Ramírez, 1 male (MACN-Ar 10263; det. C. Grismado, 2003, SEM preparations MJR-909–910); P. Nac. Lanín, Lago Huechulafquen, 7.I.1985, M. Ramírez, 1 male (MACN). Note: Indirect eyes tapeta like those of *Cupa kalawitana*, but with thinner lines. PME with well defined tapetum, longitudinal median line.

Stephanopoides brasiliana Keyserling (Thomisidae). ECUADOR: Napo: Archidona, 2.II.1983, A. Roig, 1♂ (MACN-Ar).

*Stephanopoides sexmaculata** Mello-Leitão (Thomisidae). ARGENTINA: Misiones: Dept. Cainguás, P. Prov. Salto Encantado, 27°07′S, 54°48′W, sendero al Salto La Olla, 10–11.I.2005, C. Grismado, L. Lopardo, L. Piacentini, A. Quaglino & G. Rubio, 1♀ (MACN-Ar; SEM preparations MJR-1282–1285; ARAMAR000530). Puerto Bossetti, Arroyo Uruguaí, I.1964, J.M. Viana, 1♀ (MACN-Ar; SEM preparations MJR-1286–1287).

Stephanopoides simoni Keyserling (Thomisidae). BRAZIL: Pará: Belem, Macambó, VII.1970, M.E. Galiano, 1♂ (MACN-Ar).

Stephanopoides sp. (Thomisidae). ARGENTINA: Misiones: Piñalito, XI.1954, Schiapelli and De Carlo, 3 subadult♀ (MACN-Ar; temporary mounts MJR-1319–1321).

*Stiphidion facetum** Simon (Stiphidiidae). AUSTRALIA: New South Wales: 4 mi S Glencoe, 1280 m, 29.XI.1962, E.S. Ross and D.Q. Cavagnaro, 1♀ (CAS). Tasmania: Lake St. Claire Nat. Park, Woodland Nature Walk, 42°07′S 146°10′E, under rocks, 17.V.1996, L.J. Boutin, 1♂ (CAS). OTHER SOURCES: Griswold et al. (2005).

Storenomorpha paguma Grismado and Ramírez (Zodariidae). VIETNAM: HA TINH Prov.: Huong Son District, An River, Huong Son Forest, 13 Km W Rt. 8, ca. 18°20′52″N, 105°14′41″E, (ref. HS31) 680 m, mammalogist's pitfalls, 12.V.1998, D. Silva Dávila, 1♂ (AMNH, identified by R. Jocqué, 2001; SEM preparation MJR-138); same data, 23.IV.1998, 1♂ (AMNH). Con Cuong District: (ref. NS9) ca. 5 km from Khe Bu, along stream, night, 1.V. 1998, D. Silva Dávila & Minh, 2♀ (AMNH, identified by R. Jocqué, 2001; SEM preparations MJR-102, 123). OTHER SOURCES: Jocqué and Bosmans (1989), Jocqué (1991).

*Strophius albofasciatus** Mello-Leitão (Thomisidae). ARGENTINA: Misiones: 17 de Octubre, X.1953, De Carlo, Schiapelli, Viana, Galiano, 1 male, 1 male penultimate (respiratory system examined) (MACN-Ar 3817; SEM preparation MJR-916); Misiones: no specific locality, 1943, J.M. Viana, 1♀ (MACN-Ar 1690; SEM preparations MJR-917, 920–921); Misiones: Santa María, II.1945, J.M. Viana, 1 male (MACN-Ar 2896; SEM preparations MJR-918–919). Tobuna, II.1952, W. Partridge, 1♀ (MACN-Ar; temporary mounts PMF-164–166, ARAMR000779); Manuel Belgrano, 1954, Schiapelli–De Carlo, 1 male, (MACN-Ar; temporary mounts PMF-162, 163, ARAMR000778); P. Nac. Iguazú, XI.1989, M.J. Ramírez, 1 male (MACN-Ar; expanded palp temporary mount CJG-504). Identified by C. Grismado, 2003.

*Strotarchus piscatorius** (Hentz) (Eutichuridae). USA: Massachusetts: Barnstable Co., Hatchville, FCWMA, 14.VIII.1989, R.L. Edwards, oak trunk, 1♀ (USNM; SEM preparation MJR1001); 17.VII.1990, R.L. Edwards, pine trunks, 159m, 1♀ (USNM; SEM preparations MJR1002–1004, 1006); USA: West Virginia: Preston Co., WV University Forest, Chestnut Ridge, hardwood, pitfall trap, Stand 8 Plot 13, 5–12.VI.1989, D.T. Jennings col., 1♂ (USNM; SEM preparation MJR1005). USA: Pennsylvania: NE Jamison, Horseshoe Bend, Neshaminy Cr., V.1955, W. Ivie, 4♂ 10♀ (AMNH; det. A. Bonaldo 1998).

*Syspira eclectica** Chamberlin (Miturgidae). MEXICO: Baja California Sur: nr. La Paz, VIII.1990, T. Jackson, 6♀ 3♂ together with 3♂ of different species (AMNH; SEM preparations MJR-496–500, identified by C. Grismado 2004. NOTE: the male not scanned has a bipartite median apophysis. It is not clear which males are conspecific with the females, or whether there is more than one species among the females as well. The variability in the retrocoxal hymen occurs among males of the same species as well). DOMINICAN REPUBLIC: San Cristobal: Borbon, Cuevas Pomier, tropical deciduous forest, 200 m, FIT, 13–20.VII.1995, S. and J. Peck, 5 males 1♀ 1 immature (AMNH; tapeta observed).

Systaria sp.* (Eutichuridae). VIETNAM: Ha Tinh: Huong Son District, An River, Huong Son Forest, 13 Km W Rt. 8, ca. 18°20′52″N, 105°14′41″E, 940 m, main trail, underneath tree bark, v.19.1998, D. Silva Dávila, 1♀ with spiderlings (AMNH/IEBR; SEM preparations MJR-470–475); (ref. HS7) 940 m, entomologist's pitfalls, v.15.1998, D. Silva Dávila, 2♂ (AMNH/IEBR; SEM preparations MJR-476, 477; respiratory system examined); (ref HS2) 940 m, mammalogist's pitfalls, v.12.1998, D. Silva Dávila, 1♂ (AMNH/IEBR). OTHER SOURCES: Deeleman-Reinhold (2001).

*Teminius insularis** Lucas (Miturgidae). BOLIVIA: La Paz: Apolo, 1400 m, 5–15.VIII.1989, L. Peña, 1♀ (AMNH; SEM preparations MJR-250, 251). CUBA: San Vicente, Pinar del Río, 7–8.VII.1956, C. and P. Vaurie, 1♂ (AMNH; SEM preparation MJR-252). BRAZIL: Minas Gerais: Governador Valadares, under debris, rocks, 9–13.III.1985, died 10.IV.1983, egg case taken with female, 1♀ with eggsac (AMNH; SEM preparation MJR-253). ARGENTINA: Jujuy: San Salvador de Jujuy, 17.I.1966, E. Maury, 5♀ (MACN, identified by N. Platnick and Ramírez, 1990; respiratory system examined preparation MJR-945).

*Tengella radiata** Kulczyn'ski (Tengellidae). COSTA RICA: Guanacaste: several km N of Tilaran, 700 m, rotting logs in dense forest and pasture, 12.VIII.1983, F. Coyle, J. Carico, 1♀ (in AMNH; SEM preparations MJR-514); Limón: Sector Cocori, 30 Km N Cariari 100 m, Malaise L_N_286000_567500 #4525, XII.1994, E. Rojas, 2♂ (INBIO; SEM preparation MJR-698); Cartago: Puricil, camino a P. Nac. Tapantí, fincas cafetaleras, 1500 m, 9°45′33″N 83°49′11″W, 8–11.V.2002, M. Ramírez, 1♀ (MACN), 1♂ 1 immature (MACN), 1 immature (MACN; respiratory system examined).

Teutamus sp.* (Liocranidae: *Teutamus* group). THAILAND: Nakhon Si Thammarat Prov., Khao Luang NP, 8°43′25.2″N 99°40′7.7″E, 355 m, 10–12.X.2003, ATOL Expedition 2003 1♂ 3♀ 1 juv. (ZMUC, to be distributed; SEM preparations MJR-1253–1263; IDLot NS0349; tracheae digested from immature, lost during staining).

Textricella luteola (Hickman). AUSTRALIA: Tasmania: Cradle Mountain–Lake St. Clair N.P., entry road, nr Derwent Bridge, S42°06′59.4 E146°10′31.3, 750 m, mixed forest with eucalypt, general collecting, 11.III.2006, M. Ramírez, 2♂ 1♀ (MACN-Ar; SEM preparations FML-343–347, 350–353; temporary preparations CJG-420, PMF-201–205, ARAMR000666, 793, 885).

*Thaida peculiaris** Karsch (Austrochilidae). ARGENTINA: P. Nac. Nahuel Huapi: Puerto Blest, 7–20.I.2000, L. Lopardo y A. Quaglino, 1♀ (MACN-Ar 9976; SEM preparations MJR-675, 676, 839); same data, 1♀ (MACN-Ar 9977). CHILE: Cautín: Bellavista, N shore Lago Villarrica, 310 m, site 655, window trap, Valdivian rainforest, 15–30.XII.1982, A. Newton & M. Thayer, 1♂ (AMNH; SEM preparation MJR-765). Osorno: P. Nac. Puyehue: Aguas Calientes, 13–17.XII.1998, M. Ramírez, L. Compagnucci, C. Grismado, L. Lopardo, early spiderlings, stage without hairs, with part of the egg membrane (MACN-Ar; SEM preparations MJR-61, 64, fixed 25.XII.1998).

*Thomisus onustus** Walckenaer (Thomisidae). UZBEKISTAN: Kashkadarya Area: Muborak District, Deikum sands, 1 km N of Muborak, N39°16.737′ E65°10.083′, 27.V.2003, 290 m, Site 17, L. Prendini & A.V. Gromov, 2♂ (AMNH; SEM preparations FML-401–403, temporary mounts CJG-285–286; ARAMR000315). Guzar district, Gissar Mountains, 10 km SE of Guzar, 1.5 km SE Pachkamar, 38°33.852′N 66°21.333′E, 663 m, Site 10, 17–18.V.2003, L. Prendini & A.V. Gromov, 3♀ (AMNH). Bukhara Area: Gizhduvan District, 14.5 km N of Kanimekh, SW foothills of Karatau Mountain Range, N40°24.851′, E65°08.955′, 396m, Site 28, 5.VI.2003, L. Prendini & A.V. Gromov, 1♀ (AMNH, SEM preparations FML-404–411; ARAMR000888). Jondor District, 40 km E of Gazil, in the Kyzylkum Desert, 40°07.069′N, 63°56.510′, 203 m, L. Prendini & A.V. Gromov, 29.5.2003, 3♀ (AMNH; temporary mount CJG-284; ARAMR000314). Kyzyl Orda Area: Chiili District, 16 km NE of Chiili, 6 km NE of Almaly (Plodoyagodnoe), N44°16,916′ E66°34,184′, 143 m, 22.VI.2003, L. Prendini & A.V. Gromov, 1♀ (AMNH, temporary mounts CJG-187–188; ARAMR000141), 1♂ (AMNH; temporary mounts CJG-189–190; ARAMR000142).

*Tibellus oblongus** (Walckenaer) (Philodromidae). USA: Idaho: Mesa, W116°26′, N44°38′, 2.VII.1943, W. Ivie, 2♂ 6♀ 2 juv. (AMNH; SEM preparations MJR-156, 162–164, temporary preparation MJR-1358; respiratory system examined). POLAND: Dziekanów Polskie, 25.V.1989, B. Malkin, (AMNH; SEM preparations MJR-188–190). Other sources: Homann (1975).

*Titanebo mexicanus** (Banks) (Philodromidae). USA: California: Imperial Co., Heber Dunes, southern end, Heber Rd. East of Hwy. 111, N32°42.627′, W115°23.507, 50 ft., 29.X.2000, M. Hedin, M. Lowder, J. Skejic, B. Davis, D. Wood, det. M. Hedin 2000, 4♂ 3♀ (UCSD, MCH 00_160, SEM preparations MJR-1264–1273, temporary mounts CJG-549, PMF-51–52, ARAMR000943, 693). San Bernardino Co., El Mirage Valley, SE corner, vic. Jnct. El Mirage/Mt. View Rds., N32°42.627′ W115°23.507, 50 ft., 2.V.2001, M. Hedin, M. Lowder, J. Skejic, B. Davis, D. Wood, beaten from *Atriplex* sp., det. M. Hedin 2000, 1♂ 3♀ (SDSU, MCH 01_065, temporary mounts CJG-114, PMF-53–55; ARAMR000117, 694, 695).

*Titanoeca americana** Emerton (Titanoecidae). USA: New Jersey: Lambertville, 74.26N 40.22W, VI.1952. W. Ivie 4♂ 4♀ (AMNH, identified by R. Leech).

Titidius sp. (Thomisidae). BRAZIL: Amazonas: Manaus, Reserva Ducke, VIII.1971, M.E. Galiano, ♂♀ (MACN-Ar; SEM preparations MJR-124–130).

Tmarus holmbergi Schiapelli and Gerschman* (Thomisidae). ARGENTINA: Buenos Aires: Punta Indio, 17.XI.1991. M. Ramírez, 3 males, 6♀, 1 immature (MACN-Ar; SEM preparations 922–925, respiratory system examined, temporary mounts CJG-118, 123, 283, ARAMR000122, ARAMR000313). Isla Martín García, aeropuerto, 6–8.VI.2004, C. Scioscia, F. Labarque, C. Pautasso, S. Rodríguez-Gil & S. González, ♂ (MACN-Ar 10505; male palp expanded in KOH, temporary preparation CJG-176, ARAMR 000104). Isla Martín García, bosque ribereño, 24–26.VIII.2004, C. Scioscia, A. González, A. Ojanguren & S. González, 1♂ (MACN-Ar 10520; temporary preparations CJG-152-153); same data, 1♂ (MACN-Ar 10521; temporary preparation CJG-151). Res. Natl. Otamendi, S34°13′31.1″ W58°54′00.9″, 32 m, 22.VI.2006, M. Ramírez, F. Labarque, C. Sosa, 1♀ (MACN-Ar 11032; SEM preparations FML-445–449).

Toxoniella sp.* (Liocranidae). TANZANIA: Tanga: W Usambara Mtns., Mazumbai, forest, 4°49′S 38°30′E, 1400–1800 m, 11–20.XI.1995, sifting litter, C. Griswold, N. Scharff, D. Ubick, 7♂ 9♀ 2 immatures (CAS; SEM preparations MJR-303–309).

*Toxopsiella minuta** Forster (Cycloctenidae). NEW ZEALAND: South Island: west coast, Saltwater Forest, rimu forest, Deans rd. pitfall trap, V.1991, P. Walsh, (CAS, identified by J.

Boutin, 1995; SEM preparations MJR-364–370). OTHER SOURCES: Forster (1979).

*Trachelas mexicanus** Banks (Trachelidae). USA: New Mexico: Bernalillo Co., Albuquerque, 1515 Los Arboles NW, inside house on bathroom wall, elev. 4960′, 6.X.1974, D.T. Jennings, 1♂ (AMNH, identified by D. Jennings, 1974, SEM preparations MJR-552–553); same data, on floor in living room, 1♀ (AMNH, identified by D. Jennings, 1974. SEM preparations MJR-554–558); 2812 Cagua NE, inside house in kitchen, J.W. Jennings, 1♂ (AMNH); same data, on posrch of house, 11:00 hrs, D.T. Jennings, 1♀ (AMNH). OTHER SOURCES: Platnick and Shadab (1974).

*Trachelas minor** O. P.-Cambridge (Trachelidae). "B. Sanda. Marnia!" 4♂ 4♀ (MHNP 12306). "Free Town," 2♀ 1 immature (MHNP 10715). ALGERIA: "Gl. M. Conica!" (?) many males and ♀ (MHNP 1520; SEM preparations MJR-626–632).

Trachelidae ARG* (Trachelidae). ARGENTINA: Buenos Aires: Isla Talavera, 2 km E Zárate, 3.XI.1996, M. Ramírez, 1♂ 1♀ (MACN-Ar; SEM preparations MJR-1291–1299); same data, 1♂ 1♀ (MACN-Ar; ♀ ARAMR000926, temporary mount CJG-488); same data, 1♂ 1♀ (MACN-Ar; male ARAMR000924, temporary mounts CJG-485, 486, 493; ♀ ARAMR000925, temporary mount CJG-487); same data, 4♂ 7♀ 1 subadult ♀, pharate (tracheae examined, KOH digested).

*Trachelopachys ammobates** Platnick and Rocha (Trachelidae). BRAZIL: Rio de Janeiro: restinga at Barra de Maricá, 22°57′S, 43°50′W, 38km E Río de Janeiro, 18.V.1991, C.F. da Rocha, 2♀ 4 immatures (AMNH; SEM preparations MJR-82–84); same data, diurnal on sand, 3♂ 1 penultimate male (AMNH; SEM preparation MJR-87).

*Trachycosmus sculptilis** Simon (Trochanteriidae). AUSTRALIA: New South Wales: Cow Flat, S of Bathurst, 13.XI.1988, G.S. Hunt and Education Vols, 2♂ 5♀ (AMS KS 29941; SEM preparations MJR-582–585). OTHER SOURCES: Platnick (2002).

Trochosa ruricola (De Geer) (Lycosidae). USA: New Hampshire: Durham, 18.VII.1993, killed 25.IX.1993, M. Townley, 1♀ (University of New Hampshire; SEM preparations MJR-849–852).

Uliodon cf. *frenatus** (Zoropsidae). NEW ZEALAND: North Island: Wellington town belt, top of Harriet Street, 24.IV.1995, J. Boutin, 2♂ 4♀ (CAS; SEM preparations MJR-344–347); same data, 14.IV.1996, 1♂ 2♀ (CAS; male respiratory system examined, eyes cleared).

*Uloborus glomosus** (Walckenaer) (Uloboridae). USA: North Carolina: Clemson, 82.50W 34.41N, 6.VIII.1962, A. Payne, 1♂ (AMNH, identified by W. Ivie, 1962); Mast, 10 mi W Boone, (U.S. 421), 18–24.VII.1954, E.E.B., 2♀ (AMNH, identified by Muma, 1961; SEM preparations MJR-815–817). OTHER SOURCES: Opell (1979), Griswold et al. (2005, several *Uloborus* species).

*Vectius niger** (Gnaphosidae). PARAGUAY: Chaco: Puerto Casado, 14.5.1950, A. Bachmann, 1♂ (MACN-Ar; SEM preparations MJR-1144, 1145, temporary mount CJG-507). ARGENTINA: Salta: Alemanía, Ruta Prov. 68 Km 80, entre piedras, 3.XI.2004, C.J. Grismado, L. Compagnucci, 1♀ (MACN-Ar 10808; SEM preparations MJR-1139–1143); same data, 1♀ penultimate (MACN-Ar 10809; SEM preparation MJR-1138); same data, 3 immatures (MACN-Ar; tracheae and tapeta examined); Jujuy: Yuto, El Pantanoso, 18.XI. 1966, M.E. Galiano, 1♀ (MACN-Ar; temporary mount CJG-505; ARAMR000936); same data, 1♂ (MACN-Ar; temporary mount CJG-506; ARAMR000937); same data, 1♀ (MACN-Ar; SEM preparations MJR-1146–1148).

Vulsor sp.* (Ctenidae). MADAGASCAR: Fianarantsoa: P. Nat. Ranomafana: Talatakely 21°14.9′S, 47°25.6′E, 19–30.IV.1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, J. Ranoriaranarisoa, J. Schweikert, D. Ubick, 4♀ 1♂ (CAS, identified by D. Silva Dávila; SEM preparations 619, 620, 717). OTHER SOURCES: Silva Davila (2003).

Xenoctenus sp.* (Miturgidae: *Xenoctenus* group). ARGENTINA: Santiago del Estero: Santa Catalina, 26.X.1963, M.E. Galiano, 1♂ 1♀ (MACN-Ar; SEM preparations MJR-662–664, 856); La Rioja: Embalse Los Sauces, 7–8.X.1965, E. Maury, (MACN-Ar; SEM preparations MJR-665, 667). OTHER SOURCES: Silva Davila (2003).

Xenoplectus armatus Schiapelli and Gerschman ("Gnaphosidae"). ARGENTINA: Misiones: Santa María, X.1953, Schiapelli and De Carlo, ♂ holotype MACN-Ar 4201, ♀ allotype MACN-Ar 4202, 7♂ 19♀ paratypes 3793, 4200, 4203, 4204, all examined. Misiones, no specific locality, XI–XII.19?? (illegible), J.M. Viana, 1♀ (MACN-Ar; SEM preparation MJR-131).

Xenoplectus sp.* ("Gnaphosidae"). BRAZIL: Rio Grande do Sul: Reserva do Pró-Mata, São Francisco de Paula, 2004, L. Bertoncello, 1♂ 2♀ (PUC 16367; SEM preparations MJR-987–993).

*Xiruana gracilipes** (Keyserling) (Anyphaenidae). ARGENTINA: Misiones: Dep.. Cainguás, P. Prov. Salto Encantado, 27°07′S, 54°48′W, camping, 10–12.I.2005, C. Grismado, L. Lopardo, L. Piacentini, A. Quaglino and G. Rubio, 1♀ (MACN-Ar, ARAMR182, SEM preparations MJR-1199, 1200). Santa Fe: Las Gamas, 20 km W Vera, 27–30.X.1994, M. Ramírez and J. Faivovich, det. C. Grismado 2005, 1♂ (MACN-Ar; SEM preparations MJR-1206–1209). Entre Ríos: Palmar de Colón, 18.12.1975, col. M.E. Galiano, det. A.D. Brescovit, 2003, 1♂ (MACN-Ar; ARAMR000905; temporary preparation CJG-467). Ciudad Autónoma de Buenos Aires: 21.3.2007, col. Andrés Ojanguren, det. Cristian J. Grismado 2007, 1♀ (MACN-Ar; ARAMR000904; temporary preparation CJG-466). Buenos Aires: Merlo, 12.II.2003, M. López, det. C. Crismado 2005, 1♀ (MACN-Ar, ARAMR58, SEM preparations MJR-1201–1205).

*Xysticus cristatus** (Clerck) (Thomisidae). ENGLAND: Dibden bottom Hantz (?), 5.VI.1955, 2♂ 1♀ (AMNH; SEM preparation MJR-157). DENMARK: Vorkingkoy (?) 28.V.??, 2♂ 8♀ (ZMUK; SEM preparation MJR-760). FRANCE: La Belme-sur-Cerdon, 7 km S of Nantus (Jura), 4.VI.1975, B. Malkin, 3♂ 11♀ (AMNH; SEM preparation MJR-172); Oloron, St. Marie, Pyrennees Atlantiques, 30.VI.1975, B. Malkin, 1♂ (AMNH; SEM preparations MJR-178, 179). SWITZERLAND: Rüttenen (Solothurn) 1–8.VI.1976, B. and H. Malkin, (AMNH; SEM preparations MJR-174–177).

*Zora spinimana** (Sundevall) (Miturgidae). BELGIUM: Hautes-Fagnes, Mont Rigi, station III, 1–15.VI.1977, J. Kekenbosch, 5♂ 2♀ (IRSN, identified by J. Kekenbosch, 1977; SEM preparations MJR-643–649). DENMARK: No data, many specimens (ZMUK 5715; SEM preparation MJR-759).

*Zorocrates gnaphosoides** (O. P.-Cambridge) (Zorocratidae). MEXICO: Chiapas: Surface, Los Llanos, 29.VIII.2972, Mitchell, Russell, 1♀ 1♀ subadult (AMNH; SEM preparations MJR-448–452). Identified by N. Platnick from SEM images, in litt.

*Zorocrates unicolor** (Banks) (Zorocratidae). USA: Texas: Big Bend Nat. Pk., the Basin, 6000 ft., 25.VIII.1967, W. Gertsch, Hastings, 1♂ 1♀ (AMNH, identified by N. Platnick from SEM images, in litt.; SEM preparations MJR-453, 454). MEXICO: Hidalgo: El Tablón, 7 mi SE Zimapan, 20°40′N 99°20′W, 19.VIII.1964, J. and W. Ivie, 3♂ 1 subadult ♀ (AMNH; voucher D. Silva Dávila study, 2000; respiratory system examined from subadult ♀).

*Zoropsis rufipes** (Lucas) (Zoropsidae). CANARY ISLANDS: Tenerife, XI.1975, P. Oromí, 1♀ (AMNH; SEM preparations MJR-456–459); same data, 1♂ (AMNH; SEM preparations MJR-460, 461); same data, 1♂ (AMNH, voucher D. Silva Dávila study 2000), all identified by D. Silva Dávila, 1997–1998; same data 2♀ (AMNH, identified by C. Griswold, 1990). OTHER SOURCES: Griswold et al. (2005), Bosselaers (2002).